

A REVISION OF *DIACARNUS* BURTON AND *NEGOMBATA* DE LAUBENFELS  
(DEMOSPONGIAE: LATRUNCULIIDAE) WITH DESCRIPTIONS OF NEW SPECIES  
FROM THE WEST CENTRAL PACIFIC AND THE RED SEA

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Species previously assigned to the genus *Latrunculia*, which possess discate microrhabds as the microsclere complement, have been re-evaluated and assigned to *Diacarnus* Burton and *Negombata* de Laubenfels, which both contain spinulate rather than discate microrhabd microscleres. The type species of *Diacarnus*, *Axos spinipoculum* Carter, is redescribed, and seven new species are described: *D. bellae*, *D. erythraeanus*, *D. levii*, *D. ardoukoba*, *D. bismarckensis*, *D. tubifera*, and *D. megaspinothabdosus*, spp. nov. The type species of *Negombata*, *Latrunculia corticata* (Carter), is redescribed and the only other known species, *Latrunculia magnifica* Keller, is transferred to *Negombata*. Diagnostic morphological characters which emphasize a combination of gross morphology, spicule dimensions, microsclere morphology and disposition, are identified for *Diacarnus* and *Negombata* and the affinities of these and other latrunculiids, *Latrunculia* and *Sigmosceptrella*, are compared to each other and to other demosponges. New locality and species records reveal a remarkably disjunct biogeographic distribution for *Diacarnus*: the greatest diversity of species is found in northern Papua New Guinea and in several Micronesian atolls, but the genus extends east through New Caledonia to Fiji, and south to Port Jackson in south-eastern Australia. Two species of *Diacarnus* are also found in the Red Sea. The genus has not been recorded in the published literature, nor in the extensive unpublished collections known for the Indo-Malay region. □ *Demospongiae, Latrunculiidae, Micronesia, Red Sea.*

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Sponges having discorhabds, dicasters or spinulate acanthomicrohabds as microscleres have traditionally been placed within *Latrunculia* Bocage, Latrunculiidae Topsent. Distinctive microscleres of *Latrunculia* bear four whorls of spines frequently united in a disc, on a straight axial rod, which are disposed in an erect layer above the sponge ectosome. *Latrunculia* contains massive sponges with papillae and sieve-pore areas, with skeletons of monactinal or rarely diactinal spicules arranged in an irregular reticulation of poorly defined, somewhat plumose, tracts. Other latrunculiids such as *Podospongia* Bocage, *Sigmosceptrella* Dendy, and *Barbozia* Dendy, contain acanthomicrohabds. The affinities of these genera have been diversely interpreted, resulting in allocation of the family either in the tetractinomorph Hadromerida, following Bergquist (1978), or in the ceractinomorph Poecilosclerida following Topsent (1922).

However, it is unlikely that acanthomicrohabds, which are a distinctive feature of the family as presently recognised, are homologous in all of these genera. The genus *Latrunculia*, which contains discorhabds, has received several species which are certainly atypical. Two species from the Red Sea, *Latrunculia corticata* Carter, 1879 (with its claimed junior synonym *L. magnifica* Keller, 1889), and *L. purpurea* Carter, 1881, were isolated in a new genus *Negombata* by de Laubenfels (1936), a distinction which had been suggested long ago by Ridley and Dendy (1887) and Thiele (1900). De Laubenfels differentiated these specimens from *Latrunculia* on the morphology of the microscleres which are spinulate sanidaster-like acanthomicrohabds, rather than discate as in *Latrunculia*. The position of *Axos spinipoculum* (Carter, 1879), transferred to *Latrunculia* by Hooper (1986), is doubtful. Burton (1934) proposed the new genus *Diacarnus* to receive *Axos spinipoculum* Carter in recognition of the charac-

teristic acanthomicrohabds which consisted of a straight shaft bearing four whorls of spines.

We have found several sponges in the West Central Pacific and in the Red Sea which are characterised by the possession of spinulate rhabds, hereafter termed spinorhabds. These microscleres are thin rods with spines or bumps scattered irregularly or uniformly in 4 whorls along the shaft. The microscleres of these new sponges are clearly related to those of *Axos spinipoculum* Carter, *Latrunculia* (= *Negombata*) *corticata* Carter, and *L.* (= *Negombata*) *magnifica* Keller. These species are re-evaluated in the light of this new material.

#### METHODS

Sponges were collected using SCUBA by the authors and the Coral Reef Research Foundation (CRRF), Micronesia, from Chuuk (Truk) State, Micronesia, the Australian Great Barrier Reef, northern and southern Papua New Guinea, New Caledonia, Fiji, the Philippines, the Red Sea, and the Gulf of Aden (Fig. 4). On collection, samples were preserved in 70% ethanol or in 10% formalin and prepared for histological examination as described in Kelly-Borges et al. (1994). The dried holotype of *Latrunculia* (= *Negombata*) *corticata* (Carter) was reconstituted by prolonged soaking of a fragment in dilute detergent. The colour notation for living and preserved specimens follows the Rheinhold Colour Atlas (Kornerup & Wanscher, 1961). Spicule dimensions are given as mean length (range of length measurements) times width (range of width measurements) followed by the number of spicule measurements taken. Primary type material has been deposited in the Queensland Museum, Brisbane, Australia, paratypes and fragment of holotypes, schizotypes of some authors, have been deposited in the Natural History Museum, London, and in the Muséum National d'Histoire Naturelle (Paris). Registration numbers are cited in the text.

Abbreviations used in the text: QM, Queensland Museum, Brisbane; BMNH, Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; HBOM, Harbor Branch Oceanographic Museum, Fort Pierce, Florida; SIO, Scripps Institute of Oceanography, San Diego; NSRC (UPNG), Natural Science Resource Centre, University of Papua New Guinea, Port Moresby; CRRF, Coral Reef Research Foundation, Federated States of Micronesia; OCDN, Specimen sample numbers for United States National Cancer Institute shallow-water

collection program contracted to the CRRF. A complete collection of all OCDN specimens is located at the Smithsonian Institution (United States National Museum); Q66C, Specimen sample numbers for United States National Cancer Institute shallow-water collection program previously contracted to the Australian Institute of Marine Science, Townsville. This latter collection is now located at the Queensland Museum.

#### SYSTEMATICS

##### Family LATRUNCULIIDAE Topsent

##### *Diacarnus* Burton, 1934

*Diacarnus* Burton, 1934: 549

##### TYPE SPECIES

*Axos spinipoculum* Carter, 1879: 286

##### DIAGNOSIS (emended)

Massive spherical or barrel-shaped, lobate-digitate, repent-branching, tubular or thickly encrusting Latrunculiidae. Surface with single or multiple conules or blunt broad tubercles or mounds, microscopically smooth, slippery and rubbery. Ostia radiate in stellate formation in shallow rounded depressions, oscules apical with low fleshy raised collars, frequently differentially coloured cream, always highly contracted and invisible in preserved specimens. Texture extremely tough but elastic. Colour usually pale purple-pink mottled with deep reddish brown and yellow brown, interior cream. Megascleres subtylostrogyles, with a faint subterminal swelling at proximal end, distal end oxeote or more typically strongylote. Microscleres, two size categories of spinulate acanthomicrohabds (spinorhabds), smallest category always present and disposed on and below scalloped ectosome-choanosome boundary, second larger category, disposed within the ectosome and choanosome when present. Skeletal arrangement plumoreticulate. Primary fibres, conspicuous, appearing as vertebrate ligaments in soft flesh. Megascleres are packed and arranged parallel within axis of fibre, spongin barely visible, fibre is often hollow. Multiple fine dendritic spicule tracts emanate from tip of primary fibre as it passes into ectosome in an umbelliform arrangement, fibres radiating towards surface terminating in ectosomal megasclere brushes. Primary fibres, connected by occasional short secondary fibres, or anastomosing with adjacent fibres.

Ectosome, dense, rubbery, distinct from the underlying choanosome, with layers of collencytes and collagen fibrils parallel to surface. Choanosome, dense, with a few large canals surrounded by a dense layer of contractile cells and collagen fibrils. Fibres are surrounded by a sheet of elongate cells and bundles of collagen fibrils. Sponges incubate huge, bright orange-yellow parenchymella larvae.

***Diacarnus spinipoculum* (Carter) comb. nov.**  
(Figs 1, 4A, 5A, 6A, 7A, 8A; Table 1)

*Axos spinipoculum* Carter, 1879: 286

*Diacarnus spinipoculum*; Burton, 1934: 549

*Latrunculia spinipoculum*; Hooper, 1986: 181

**MATERIAL EXAMINED**

HOLOTYPE: BMNH 1846.10.14.174 from Port Jackson, Sydney, growing on "hard objects" (Carter 1879), depth unknown, presented by J. B. Jukes, Esq (Fig. 1).

ADDITIONAL MATERIAL: BMNH 1994.5.22.3, west side of East Fayu Island, Chuuk State, 8°32.61'N, 151°20.01'E, on ledge on outer wall, 24.4 m, collected by P. L. Colin, CRRF, 14 January 1994; BMNH 1994.5.22.4: East Fayu Island, Chuuk State, 8°32.61'N, 151°20.01'E, oceanside, on vertical wall, 10m, collected by P. L. Colin, CRRF, 14 January 1994; BMNH 1994.8.20.1, (fragment of OCDN 2559-Q): Blast Pass, 27m, Fiji Islands, collected by C. Arneson, CRRF, 20 August 1994; *Negombo tenuistellata* Dendy - BMNH 1907.2.1.28.

**DESCRIPTION**

Large spherical or oval barrel-shaped, (Fig. 5A), up to 50cm high, 40cm diameter, with a deep apical central atrium, 4-5cm diameter. Several sponges can be joined basally. Oscules, scattered on interior walls of atrium. Surface, heavily tuberculate to mammillate (conulose in the preserved holotype due to shrinkage), rubbery and microscopically smooth to touch, compressible, elastic in life, barely compressible in alcohol. Colour in life, mahogany brown (8E7), mottled with pale pinkish red (8C7), rim of apical atrium and atrium walls cream-white. Cream in ethanol.

*Skeleton*. Large primary fibres, 500-900µm diameter, radiate towards sponge surface, connected by rare short secondary fibres, 250-300µm diameter, or anastomosing with adjacent primary fibres in deeper choanosome (Fig. 6A). Primary fibre tip divides into an umbel of numerous slender dendritic spicule tracts, 38-70µm diameter, where the primary fibre passes through ectosome-choanosome boundary. Dendritic spicule tracts occasionally branch below surface and diverge and ramify within ectosome, where they

form slightly fanned brushes after narrowing to 5-10µm or only 1-4 spicule widths. Megascleres form a palisade of brushes between dendritic tract brushes. Megascleres, scattered singly or in groups of 1-3 spicules, in a vaguely radiate to confused arrangement interstitially between primary fibres. Larger thicker microscleres are scattered predominantly around edges of exhalant canals in choanosome, around ectosomal lacunae, and just below lower boundary of ectosome where smaller thinner spinorhabds are also found. Ectosome, 1200-1500µm deep, extremely dense with parallel collagen fibrils, easily distinguished from underlying choanosome which is dense and soft.

*Spicules*. *Megascleres*. Subtylostrogyles with slight subterminal swelling: 266(232-305) x 4(2-7)µm (see Table 1).

*Microscleres*. Spinorhabds I: extremely fine with small sharp spines scattered along shaft; 46(37-55) x <1µm, n=10 (Fig. 7A). Spinorhabds II: with four groups of spines, terminal spines frequently strongly recurved, central spines irregular in shape and length; 57(53-65) x 2(1-5)µm, n=20 (Table 1, Fig. 8A).

**SUBSTRATE, DEPTH RANGE, ECOLOGY**

Solitary, on oceanside reef slopes, from 10 to 27m depth.

**GEOGRAPHIC DISTRIBUTION**

Port Jackson, Sydney; East Fayu Island, Chuuk State, Micronesia; Fiji Islands (Fig. 4A).

**REMARKS**

The holotype was described by Carter (1879), and more recently by Hooper (1986), as an "elongate, subcylindrical, solid, cup-shaped with an apical depression" (Fig. 1). Examination of new material from Micronesia, and Fiji, reveals that the species has a large, deep, central atrium in life, with oscules opening into the atrium. The holotype would have almost certainly been spherical or barrel-shaped in life, with a restricted base of attachment as in the fresh material, but the specimen is now compressed laterally within the confines of the container. The surface of the preserved sponge is tuberculate but in life the tubercles are more distinctly mammillate.

Carter (1879) emphasised the characteristic "chondroid" nature of the thick ectosome and the extremely thick, tough fibres set in a relatively soft, compressible choanosome (Fig. 6A). This later feature was not emphasised in Hooper's description, based as it was on an inadequate

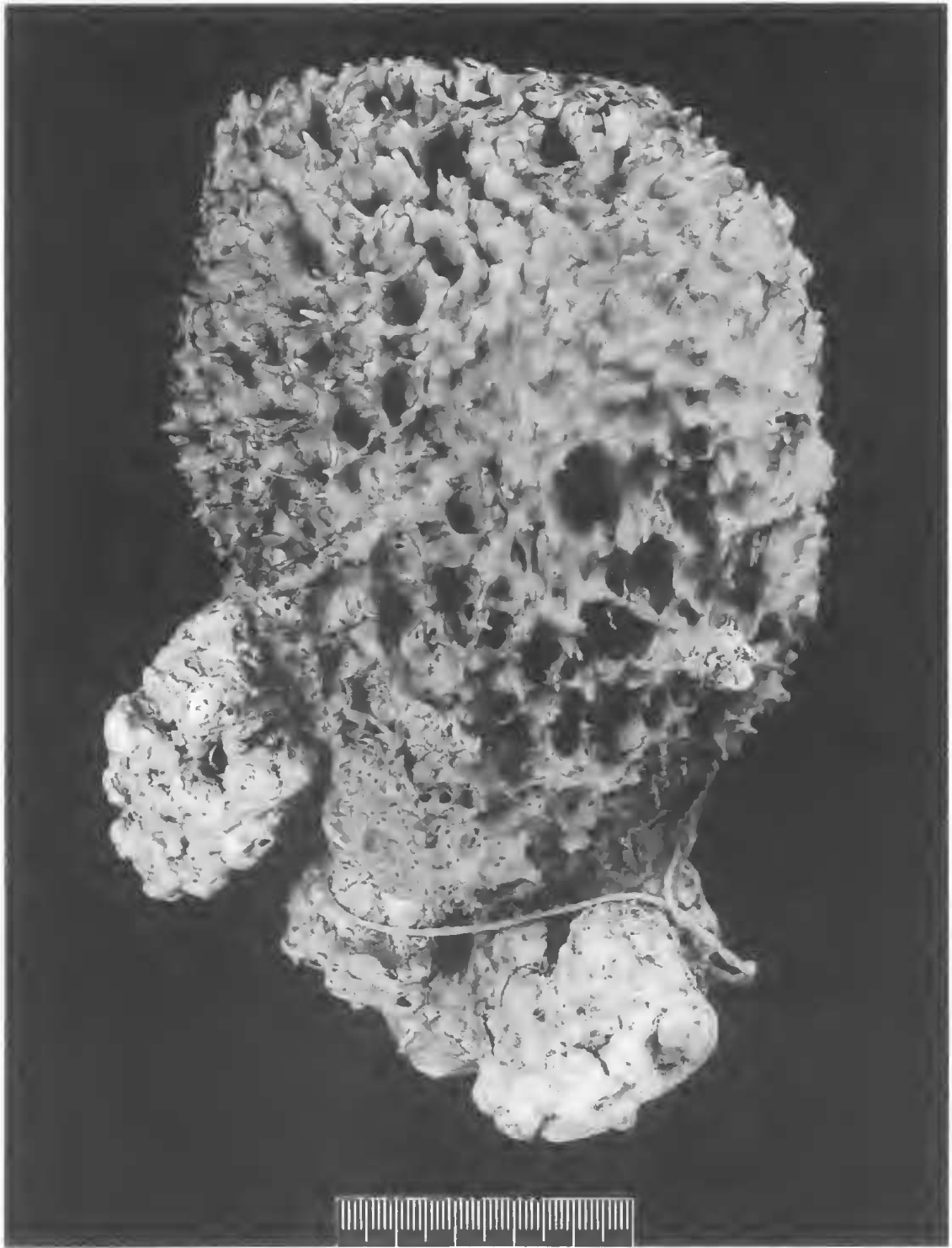


FIG. 1. *Diacarnus spinipoculum* (Carter), preserved holotype BMNH 1846.10.14.174, Port Jackson, Sydney. Scale: 5cm.



TABLE 1. Spicule dimensions of *Diacarnus spinipoculum* (Carter) and *Diacarnus bellae* sp. nov., given as mean length(range), mean thickness (range), all in  $\mu\text{m}$ .

	Megascleres	Spinorhabs I	Spinorhabs II
<i>Diacarnus spinipoculum</i> (Carter) Holotype BMNH 1846.10.14.174	277(232-305) 6(4-7)	53(50-55) <1	60(53-65) 5(2-5)
BMNH 1994.5.22.3	255(240-269) (3.5-5)	42(38-48) <1	55(53-60) (1-2)
BMNH 1994.5.22.4	266(250-278) (2-5)	43(37-46) <1	55(53-60) (1.5-2.5)
<i>Diacarnus bellae</i> sp. nov. Holotype fragment BMNH 1994.5.22.7	269(250-280) (2.5-5)	42(36-45) <1	46(43-50) (2-3)
BMNH 1994.5.22.9	280(250-300) (2.5-3)	45(40-50) <1	45(40-48) (1-2.5)
BMNH 1994.5.22.11	270(250-290) (2.5-5)	absent	44(40-48) (1-2)

older histological section of the holotype, and so the most diagnostic field characteristic of the sponge had not been reported in recent literature. The unusual and characteristic skeletal arrangement of the umbelliform primary fibres within the ectosome, observable only with detailed serial histological sectioning, was also not possible to detect in the slide of the holotype, nor were the two size categories of microscleres. The ectosomal megasclere brushes are paratangential in orientation in the holotype slide (Hooper, 1986) but are vertical, as in the living sponge, where the ectosome has not been squashed due to confinement in its container.

Two specimens from East Fayu Island have been assigned to *Diacarnus spinipoculum* (Carter) even though the spicule dimensions are slightly different from the holotype; there is considerable variation between all specimens examined and spicule dimensions cannot be considered alone in differentiation of species in *Diacarnus*. Even though the spicule dimensions of these specimens are slightly more similar to the later described *D. bellae*, spicule morphology is very different and identical to that of *D. spinipoculum*.

In a revision of *Axos* Gray from north-western Australia, Hooper (1986) transferred *Axos spinipoculum* to *Latrunculia*, considering the general skeletal features of *A. spinipoculum* to be similar to those of *Latrunculia* s.s. The type species of *Latrunculia*, *L. cratera* Bocage 1869, has several characteristic features described clearly by Bocage (1869), and later recognised by Ridley and Dendy (1887) in the descriptions of *Latrunculia apicalis* and *L. brevis* (Ridley & Dendy, 1886). Diagnostic features include the

possession of dicastra, which form a single ectosomal layer of erect spicules, their bases implanted in the dermal membrane (Fig. 9D). The dicastra or discorhabs of *Latrunculia* s.s. have two central whorls of serrated discs that are usually of unequal diameter and which are invariably located closer to either end of the spicule. The ectosomal arrangement of the dicasters is well illustrated by Bocage (1869; pl. 11, fig. 2b) and the variety of dicasters in *Latrunculia* obvious in the illustrations of Ridley and Dendy (1887) and Bergquist (1968: 18, fig. 2). The megasclere skeleton is typically a wispy loose irregular reticulation of indistinct tracts, megascleres

are styles, and microscleres are discorhabs. The surface of *Latrunculia* has characteristic mammiform ostial sieve-plates. The transfer of *Axos spinipoculum* to *Latrunculia* by Hooper (1986) is therefore invalid, as it differs considerably in the form and disposition of the microscleres, the form and disposition of the fibre skeleton, mesohyl matrix construction and in surface morphology.

Hooper (1986) also suggested *Axos spinipoculum* and *Negombo tenuistellata* Dendy 1905 from Ceylon are synonymous but conceded that the microscleres of the former are more regular than those of *Negombo*. Examination of *N. tenuistellata* (BMNH 1907.2.1.28) and histological sections of this sponge, reveal that it is very different in morphology and spiculation from *A. spinipoculum*: *N. tenuistellata* is a series of compressible thin-walled coalescent tubes, the skeleton of which consists of large gently curved styles in confused longitudinal tracts, reminiscent of the halichondroid organisation, with minute microspined sanidaster-like microscleres scattered interstitially and in a dermal membrane (Fig. 8H). The microscleres of *N. tenuistellata* are acanthose microrhabs with irregular whorls of spines along the shaft, and are much smaller than the microscleres of the *Latrunculiidae*. *Axos spinipoculum* and *N. tenuistellata* are not synonymous and neither have microscleres typical of *Latrunculia* s.s. *Negombo* was incorrectly placed in the Spirastrellidae by Dendy (1905), there is no evidence of spiralling along the shaft of the spicule. De Laubenfels (1936: 132) used the name *Negombo* for an alleged desmoxiid sponge. This genus name has not been used since, to our knowledge.

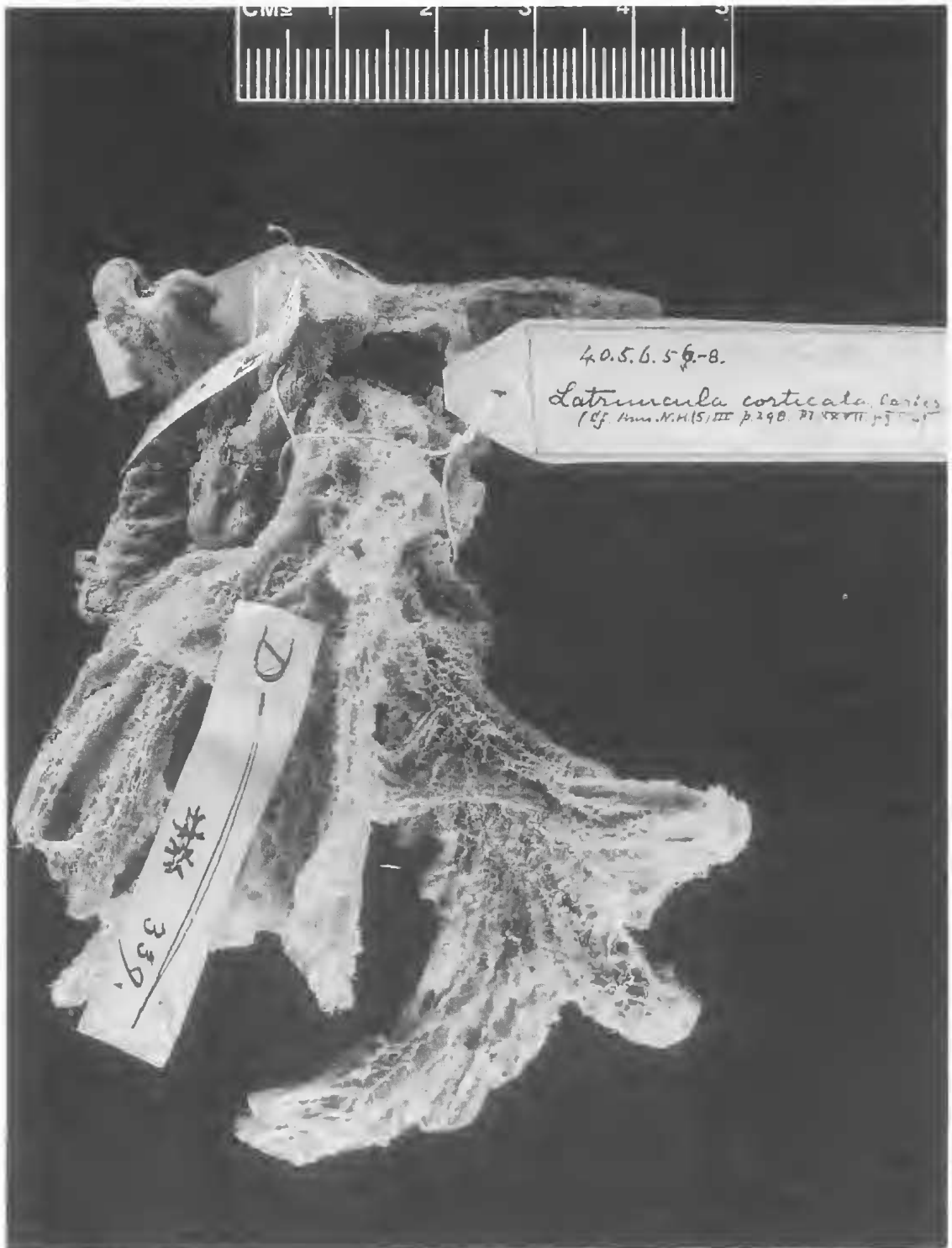


FIG. 2. *Negombata corticata* (Carter), dry holotype BMNH 1840.5.6.56-58, three dried fragments of the same specimen, Red Sea. Scale: 5cm.

***Diacarnus bellae* sp. nov.**

(Figs 4B, 5B, 5C, 6B, 7B, 8B; Table 1)

**MATERIAL EXAMINED**

**HOLOTYPE:** QMG305007: Anaw Wall, oceanside of reef west of Anaw Channel, northwest side of Chuuk Atoll, Micronesia, 7°34.24'N; 151°40.19'E, 24m, collected by P. L. Colin, CRRF, 7 August 1993; **FRAGMENT OF HOLOTYPE:** BMNH 1994.5.22.7.

**ADDITIONAL MATERIAL:** BMNH 1994.5.22.11 (fragment of OCDN 120-O): west side of Nama Island, 30 nautical miles east of Chuuk Atoll, Micronesia, 6°59.70'N, 152°34.40'E, 10m, collected by P. L. Colin, CRRF, 3 June 1992; BMNH 1994.5.22.9 (fragment of OCDN 321-I): oceanside reef, south of northeast Pass, Chuuk Atoll, Micronesia, 7°29.55'N, 151°59.10'E, 12m, collected by P. L. Colin, CRRF, 8 July 1992; BMNH 1994.5.22.19 (fragment of SIO-POH 93-005), Pohnpei, Micronesia, collected by Mary Kay Harper, SIO; BMNH 1994.6.14.1 (fragment of OCDN 2503-G): South Pass Pinnacle, west of South Pass, Chuuk Atoll, Micronesia, 30 m, 7°13.49'N; 151°46.25'E, collected by P. L. Colin and P. Schupp, CRRF, 14 June 1994.

**DESCRIPTION**

Sub-spherical, solitary sponges (Fig. 5B), 6-8cm diameter, frequently coalescent with adjacent sponges forming a spreading mat up to 60cm wide (Fig. 5C). Surface with low blunt conules 1-5mm high, separated by 5-7mm, sponge smooth, rubbery, ostia in differentially pigmented stellate depressions. Oscules, apical, single or aligned in rows, with raised cream-coloured rims. Texture, compressible but firm, elastic. Colour in life, dull rose (9D6) mottled with oxblood red (9E6), large irregular areas and ostial depressions are oak brown (5D6). Colour of oscule rims cream (4A2), in ethanol, uniformly dull yellowish brown (5B4).

**Skeleton:** Arrangement plumoreticulate, with very thick rigid multispicular fibres, 500-1225µm diameter. Secondary fibres, 100-200µm diameter, sparse, connect primary fibres to form an extremely elongate mesh. Megascleres, arranged parallel to axis of fibre, spongin barely visible, largest fibres are hollow. Megascleres, scattered interstitially in choanosome. Curved branched tracts, 10-30µm diameter, emanate from tips of primary fibres, diverge and ramify dendritically through ectosome towards surface, forming fanned brushes (Fig. 6B). Megascleres form a sparse erect to fanned palisade in outer ectosome, juxtaposed upon primary fibre brushes. Thicker category of spinorhabds, found occasionally within megasclere surface brushes, lining ectosomal lacunae in greater density, and

are common within choanosome, particularly lining canals. Thinner microscleres, found only below lower ectosomal boundary. Ectosome, 1225 to 1700µm deep. Choanocyte chambers, approximately 25µm diameter.

**Spicules, Megascleres.** (Table 1): Subtylostrogyles: 273(240-300) x (3-5)µm, n=50.

**Microscleres.** (Table 1): Spinorhabd I: extremely fine with bumps or very short spines scattered irregularly along shaft: 45(36-50) x <1µm, n=50 (Fig. 7B); Spinorhabd II: straight, with distinct short spines along shaft, in four whorls, or irregularly distributed spines (Fig. 8B). Degree of spination varies between specimens: 45(40-60) x 1-3µm, n=100.

**GEOGRAPHIC DISTRIBUTION**

Chuuk Atoll, Nama Island, and Pohnpei Island, Micronesia (Fig. 4B).

**SUBSTRATE, DEPTH RANGE, ECOLOGY**

Common on oceansides of atoll and island fringing reefs down to 30m, growing openly under full illumination.

**ETYMOLOGY**

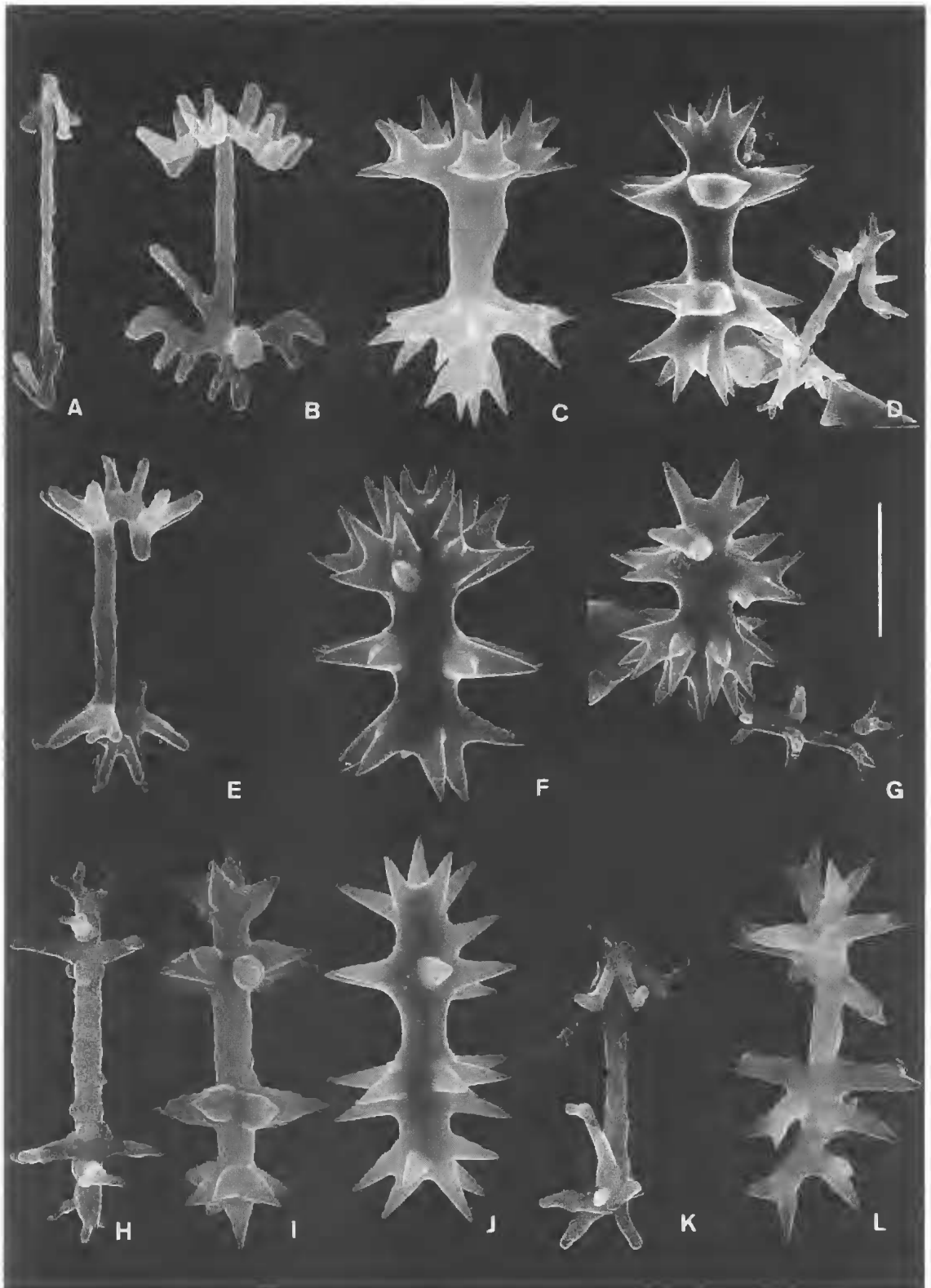
For Lori J. Bell, Coral Reef Research Foundation, Chuuk, Micronesia.

**REMARKS**

*Diacarnus bellae* and *D. spinipoculum* are very similar histologically, although the megascleres and microscleres are consistently slightly smaller and thinner in *D. bellae*. The two species can be easily differentiated by their gross morphology, however. *Diacarnus spinipoculum* is a very large barrel-shaped sponge with a wide, deep, central atrium lined with exhalant apertures. *Diacarnus bellae* is never tubular and occurs consistently in the field as a small solitary, semi-spherical sponge, or as several which coalesce to form a loose cluster. There is no suggestion of an apical atrium in *D. bellae*, the oscules are small and arranged serially or in clusters around the apex of each sponge.

***Diacarnus erythraeanus* sp. nov.**  
(Figs 4C, 5D, 5E, 6C, 7C; Table 2)**MATERIAL EXAMINED**

**HOLOTYPE:** QMG305008: near northern entrance of Obhor Creek, 30m, Djeddah, Red Sea, 21°50'N, 39°10'E, collected by J. Vacelet, 23 February 1983; **FRAGMENT OF HOLOTYPE:** BMNH 1995.6.26.1; MNHN DJV51.





ADDITIONAL MATERIAL: MNHN DJV52: fore reef zone, free living on the sand and embodying a piece of rope, 30m, King Saud Palace, Djeddah, 21°70'N, 38°80'E, collected by J. Vacelet, 8 March 1983; BMNH 1994.5.22.17: Râs Muhammad, 2-10m, South Sinai, Red Sea, dry specimen collected by Loya, 1977 (Loya 11); MNHN DJV53: Râs Muhammad, South Sinai, Red Sea, collected by Loya, 1978 (Loya 254); MNHN DJV54: Harvey Reef, 10m, near Port Sudan, collected by C. Wilkinson, August 1978; BMNH 1978.12.14.2: Harvey Reef, 10m, near Port Sudan, C. Wilkinson, August 1978.

#### DESCRIPTION

Repent or erect branches, 20-30mm diameter (Fig. 5D), variable length and branching pattern, often with slightly enlarged ends up to 50mm diameter, often anastomosing to form a sprawling mass up to 1m diameter, frequently free living on sand (Fig. 5E) or attached to debris. Texture, tough, just compressible, elastic. Surface, irregular with broad blunt conules, 2 mm high, on ends of branches. Ostia, 40-60µm diameter, localized in groups of about 10 in small surface depressions. Oscules, 2-3mm diameter, found on upper surface of branches or at tips of enlarged branch ends when in upright position, opening at end of raised cream-coloured fleshy collars. Colour, rose pink (9D6), mottled with oak brown (5D6) on surface, darker brown in approximately hexagonal concave depressions surrounded by cream ridges, more uniformly brown near end of branches. Interior in life and whole sponge in ethanol, cream (4A2).

#### SKELETON

Primary fibres, 500-800µm diameter, up to 1800µm in centre of branch, radiate towards sponge surface, connected by sparse short secondary fibres, 270-420µm diameter. Megascleres, scattered interstitially in choanosome. Curved tracts, 30-50µm diameter, less than 20µm diameter when crossing ectosome-choanosome boundary, emanate from tips of primary

fibres, diverge and ramify dendritically through ectosome, occasionally dividing just below surface, giving rise to brushes (Fig. 6C). Megascleres, form an erect to fanned palisade juxtaposed upon ectosomal brushes. Spinorhabds, rarely present, distributed just below the ectosome in upper choanosome, larger category absent. Ectosome, 600-900µm deep, distinct, rubbery. Choanocyte chambers, approximately 25µm diameter.

*Spicules*. *Megascleres* (Table 2). Subtylostrogyles, straight, with a very faint swelling of proximal end, distal end rounded: 240(190-269) x (2.5-4.8)µm, n=30.

*Microscleres* (Table 2). Spinorhabds I: straight, with occasional swellings or short spines scattered along shaft and near apices, occasional to rare: 25(24-30) x 0.8-1.3µm, n= 25 (Fig. 7C).

#### GEOGRAPHIC DISTRIBUTION

South Sinai, Eilat, Harvey Reef off Port Sudan, Red Sea (Fig. 4C).

#### SUBSTRATE, DEPTH RANGE, ECOLOGY

Common on coral substrate or rocks, large specimens, free living or attached to small corals fragments in sand. Depth range, 10-30m, although reported to be very common at Eilat in shallow water of 2-10m (Loya, pers. comm, 1978). Parenchymella larvae, 2mm diameter, within choanosome of MNHN DJV52.

#### ETYMOLOGY

The species name indicates that the sponge is found only in the Red Sea.

#### REMARKS

This sponge is easily recognised in the field by its external morphology of repent anastomosing branches, mottled surface colouration, conulose surface and smooth rubbery texture, and tough internal fibres. The small thin spinorhabds are

FIG. 3. Comparison of the developmental and mature stages of spinorhabd microscleres of *Sigmosceptrella*, *Diacarnus* and *Negombata*. A-D, *Sigmosceptrella fibrosa*, Dendy (BMNH 1925.11.1717), Maria Island, Tasmania: A, B, rhabd in earliest stage with strongly recurved spines similar to those of *Negombata magnifica* (K-L). C, the maturing spinorhabd shows signs of the fused recurved spines on the shaft, D, mature spinorhabd with a distinctly sigmoid rhabd on the right. Scale: A: 9.1µm; B: 6µm; C: 10.4µm; D: 18.2µm. E-G, *Sigmosceptrella quadrilobata* Dendy (E-100, X-371), Tuléar, Madagascar. E, specimen E-100, sigmoid rhabd, F, specimen X-371, mature spinorhabd. G, specimen X-371, mature spinorhabd with post-fusion sigmoid rhabd. Scale: E: 9.1µm; F: 16.5µm; G: 18.2µm. H-J, *Diacarnus ardoukoba* sp. nov., holotype QMG305010. H, spinulate rhabd, I, maturing spinorhabd, J, mature spinorhabd. Scale: H: 9.1µm; I: 18.8µm; J: 14.6µm. K-L, *Negombata magnifica* (Keller), MNHN DJV 56. K, rhabd with irregular sharply re-curved spines. L, mature spinorhabd. Scale: K: 5.2µm; L: 8µm.

TABLE 2. Spicule dimensions of *Diacarnus erythraeanus* sp. nov., given as mean length (range), width, all in  $\mu\text{m}$ .

Sample	Megascleres	Spinorhads I
<i>Diacarnus erythraeanus</i> QMG305007 Holotype	253(200-285) (2.6-3.5)	23.3(15-27.5) (1)
MNHN DJV52	273(235-325)	22.5 (20-25)rare
MNHN DJV53	258(195-290)	24.7(10-30)
BMNH 1994.5.22.17	251(200-300) (2.5-2.7)	23.7(12.5-30)rare (0.8-1.3)
MNHN DJV54	249(210-269) (2.4-4.8)	absent
BMNH 1978.12.14.2	243(211-269) (2.4-4.8)	absent

rare and are easily overlooked in spicule preparations and histological sections.

***Diacarnus levii* sp. nov.**  
(Figs 4A, 5F, 6D, 7D; Table 3)

**MATERIAL EXAMINED**

HOLOTYPE: QMG305009; (ORSTOM R1524), St. 478, lagoon, Belep, New Caledonia, 4-25m, 19°34.03'S, 163°42.03'E, 8 March 1990; FRAGMENT OF HOLOTYPE: BMNH 1994.5.22.16; MNHN DCL3659.

ADDITIONAL MATERIAL: MNHN DCL3660: (ORSTOM R767), St. 206, Banc de la Torche, New Caledonia, 35m, 22°56.60'S, 167°40.00'E; MNHN DCL3661: (ORSTOM R879), St. 184, 18-25m, lagoon ilot Ua, New Caledonia, 22°43.00'S, 166°49.10'E, 28 June 1979; MNHN DCL3662: (ORSTOM R994), St. 225, 42m, Canala Pass, New Caledonia, 21°18.80'S, 165°57.25'E; MNHN DCL3663: (ORSTOM R1247), St. 270, 8m, Kouare lagoon, New Caledonia, 22°46.50'S, 166°47.90'E, 3 March 1980; MNHN DCL3664: (ORSTOM R1291), St. 303, 6m, fore-reef zone, Cook Reef, New Caledonia, 19°45.60'S, 161°41.40'E, 23 June 1981; MNHN DCL3665: (ORSTOM R1528), St. 448, 6-15m, fore-reef zone, Abore reef, New Caledonia, 22°20.00'S, 166°13.15'E; BMNH 1994.5.22.15 (fragment of Q66C-0248): west side of seaward vertical wall of reef, 18m, Big Broadhurst Reef, Great Barrier Reef, Australia, 18°56.67'S, 147°43.86'E; BMNH 1994.5.22.8 (fragment of Q66C-0890): Black Reef, Whitsunday Islands, Great Barrier Reef, 10m, collected by M. Kelly-Borges, 20 October 1987.

**DESCRIPTION**

Thick erect digitations or lobes, 30-45mm diameter, anastomosing in large masses (Fig. 5F). Texture, tough, just compressible, elastic. Surface, with low rounded conules, approximately 2 mm high, 2-5mm apart. Ostia, 50 $\mu\text{m}$  diameter,

found in small, darker surface depressions. Oscules, on apices of digitations, surrounded by a white margin, 10mm diameter in preserved specimens. Surface with rounded depressions containing ostia in stellate arrangement. Colour in life oak brown (5D6), darker in ostial depressions, mottled with cream (4A2) in surface patches and around oscule margin; cream interior, uniformly white in ethanol.

**Skeleton.** Plumoreticulate arrangement with very thick multispicular fibres, 700-1125 $\mu\text{m}$  diameter, joined by small short secondary fibres, 250-375 $\mu\text{m}$  diameter, at right angles to primary fibres (Fig. 6D). Small dendritic tracts, 30-50 $\mu\text{m}$  diameter, emanate from tip of fibre, dividing and radiating through ectosome toward surface, ending in narrow brushes, surface raised in large blunt conules. Megascleres form an erect palisade at surface. Interstitial megascleres, abundant. Spinorhads, rare, found only in superficial layers of choanosome when present. Ectosome, thick, 500-1100 $\mu\text{m}$ , composed of parallel collagen fibrils in wavy bundles. Choanocyte chambers, 20 to 25 $\mu\text{m}$  diameter.

**Spicules.** *Megascleres.* (Table 3); Subtylostrongyles, with slight swelling at proximal end; 258(210-300)  $\times$  2-5 $\mu\text{m}$ , n=30.

*Microscleres.* (Table 3): Spinorhabd I: straight, with swellings or small, irregular spines usually more developed near apices, always rare, may be absent in some specimens: 58(53-60)  $\times$  0.5-2.4 $\mu\text{m}$ , n=10 (Fig. 7D).

**SUBSTRATE, DEPTH RANGE, ECOLOGY**

Found on fringing coral reef slopes down to 35m. Large embryos or parenchymella larvae, up to 1.5mm diameter, white or yellow in the choanosome, are observed in all specimens.

**GEOGRAPHIC DISTRIBUTION**

New Caledonia; northeastern Great Barrier Reef, Australia (Fig. 4A)

**ETYMOLOGY**

For Professor Claude Lévi.

**REMARKS**

*Diacarnus levii* appears to be fairly common in New Caledonia, but has only been collected from two locations on the Great Barrier Reef. In both locations the sponge was rare. Specimens from the Whitsunday Islands and Big Broadhurst Reef, Australia, have slightly larger megascleres and the spinorhads are slightly thicker with better developed spines, however, they are similar to the

TABLE 3. Spicule dimensions of *Diacarnus levii* sp. nov., given as mean length (range), width (range), all in  $\mu\text{m}$ .

Sample	Megascleres	Spinorhads I
<i>Diacarnus levii</i> Holotype QMG305009	247(190-280) (2.4-3.0)	59(55-62.5) (0.5-1.0)
MNHN DCL3663	248(245-315) (2.5-3.0)	not found
MNHN DCL3665	252(211-278) (2.4-5.0)	59(58-60) rare (0.5-1.0)
BMNH 1994.5.22.15	245(240-288) (2.0-5.0)	58(53-60) (0.5-1.0)
BMNH 1994.5.22.8	266(240-288) (2.0-5.0)	57(53-60) (0.5-1.0)

New Caledonian specimens in all other aspects. *Diacarnus levii* is differentiated from the Red Sea species, *D. erythraeanus*, by gross morphology; *D. levii* is more massive than *D. erythraeanus* which is ramose and branching. The major spicule difference between *D. levii* and *D. erythraeanus* is that the spinorhads in the former are almost twice as long as those of *D. erythraeanus*.

***Diacarnus ardoukoba* sp. nov.**

(Figs 3H, 3I, 3J, 4C, 5G, 6E, 7E, 8C)

**MATERIAL EXAMINED**

HOLOTYPE: QMG305010, Musha island, Djibouti, Gulf of Aden, 11°42.50'N, 43°08.40'E, fore reef zone, several specimens observed, some free living on sand, 24m, collected by J. Vacelet, 5 January 1985 (M 8); FRAGMENT OF HOLOTYPE: BMNH 1994.5.22.14, MNHN DJV55.

**DESCRIPTION**

Curved erect or repent branches (Fig. 5G), separate or forming a sprawling mass up to approximately 50cm long, uniform 1.5-2.0cm diameter. Ends of branches markedly conulose, branch surfaces irregularly bumpy with occasional conules, texture compressible, rubbery. Oscules distributed along branches rather than at tips of branch. Colour in life pale pink mottled with dark pink in surface depressions, uniformly cream in ethanol (4A2).

**Skeleton.** Primary fibres, 300-1000 $\mu\text{m}$  diameter, radiate towards sponge surface, connected by abundant secondary fibres, 60-300 $\mu\text{m}$  diameter. Six to ten short compact fibres, 30-70 $\mu\text{m}$  diameter, radiate from tip of primary fibre, occasionally branching to form irregular sparse surface brushes (Fig. 6E). Megascleres form an irregular and often paratangential palisade between fibres.

Megascleres, abundant in choanosome. Ectosome, generally 300 $\mu\text{m}$  deep, ranging from 120 to 540 $\mu\text{m}$ . Microscleres, two categories, smaller dispersed under ectosome-choanosome boundary, larger microscleres form a dense layer in middle of ectosome (Fig. 6E), scattered throughout choanosome particularly around canals, never found on the outer layer of ectosome.

**Spicules.** Megascleres: Subtylostrongyles: 255(220-288)  $\times$  2.4-6 $\mu\text{m}$ , n=30.

Microscleres. Spinorhabd I: spines are very irregular in shape and disposition, terminal spines occasionally bifurcate, central shaft bumpy, two major whorls of spines are evident, and closer to ends of spicule rather than regularly spaced along axis as in second category: 29(24-34)  $\times$  2.4 $\mu\text{m}$  (Fig. 3H, 7E); Spinorhabd II: conical spines are typically disposed in irregular whorls along shaft, inner two being usually a greater distance apart than each are to terminal spine cap (Fig. 3I, 3J, 8C). Terminal spine cap and outer whorl frequently merge, these spicules are often shorter than those with equally spaced whorls: 54(48-67) $\mu\text{m}$ , n=10, total maximum width 19-31 $\mu\text{m}$ , shaft diameter 2-4.5 $\mu\text{m}$ .

**GEOGRAPHIC DISTRIBUTION**

Known only from Djibouti, Gulf of Aden (Fig. 4C).

**SUBSTRATE, DEPTH RANGE, ECOLOGY**

Specimens free-living on sand at 24m deep. Reproductive mode, possibly fragmentation and release of parenchymella larvae as in other species of *Diacarnus*.

**ETYMOLOGY**

For the "Ardoukoba" expedition during which specimens were collected.

**REMARKS**

External morphology is similar to *D. erythraeanus*, which is also ramose and branching. This latter species forms mats of anastomosing branches which typically have enlarged ends upon which the oscules are located. Specimens of *D. ardoukoba* are separate, elongate branches, uniform in diameter, with flush oscules along each branch. Histologically, *D. ardoukoba* is distinct from *D. erythraeanus*, as it has a comparatively thin ectosome and less robust fibres which form a rather tighter meshed skeleton than in *D. erythraeanus*. The fibres which diverge from the apex of the primary fibres in *D. ardoukoba* are comparatively thick and short and much reduced

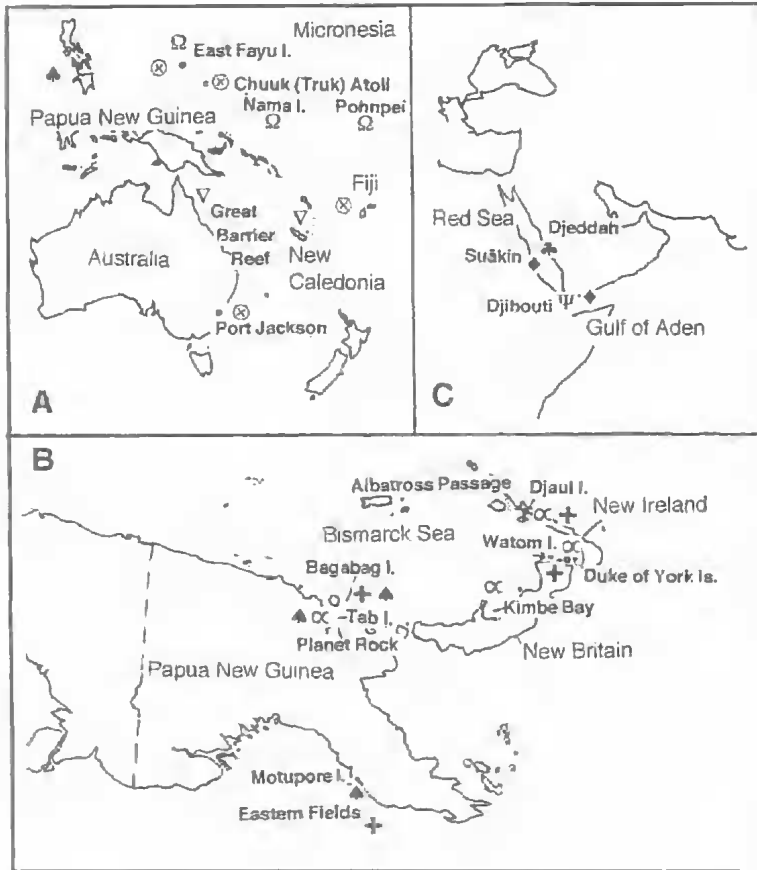


Fig. 4. Geographic distribution of *Diacarnus* spp. and *Negombata* spp. A. Indo-West Pacific and Australia:  $\odot$  *Diacarnus spinipoculum* (Carter);  $\Omega$  *Diacarnus bellae* sp. nov.;  $\nabla$  *Diacarnus levii* sp. nov.  $\blacktriangle$  *Diacarnus megaspinorhabdosa* sp. nov. B. Papua New Guinea:  $\times$  *Diacarnus bismarckensis* sp. nov.;  $+$  *Diacarnus tubifera* sp. nov.;  $\blacktriangle$  *Diacarnus megaspinorhabdosa* sp. nov. C. Red Sea and Gulf of Aden:  $\clubsuit$  *Diacarnus erythraeanus* sp. nov.;  $\Psi$  *Diacarnus ardoukobaie* sp. nov.;  $\blacklozenge$  *Negombata magnifica* (Keller).

in number compared to those of *D. erythraeanus*. The major difference on which these two species are separated, however, is the presence of a second category of spinorhabd - a larger, more robust and heavily spined microsclere, which is disposed in a mid-ectosomal layer.

***Diacarnus bismarckensis* sp. nov.**  
(Figs 4B, 5H, 6F, 7F, 8D)

**MATERIAL EXAMINED**

**HOLOTYPE:** QMG305011: (fragment of OCDN 705-Y): Planet Rock, 15m, south of Madang, northern Papua New Guinea,  $5^{\circ} 15.475'S$ ,  $145^{\circ} 49.12'E$ , col-

lected by P. L. Colin, CRRF, 6 November 1992; FRAGMENT OF HOLOTYPE: BMNH 1994.5.22.13.

**ADDITIONAL MATERIAL:** BMNH 1994.5.22.12 (fragment of OCDN 754-C): Banban reef (uncharted), 20m, Kimbe Bay, West New Britain, Papua New Guinea,  $4^{\circ} 55.53'S$ ,  $150^{\circ} 55.51'E$ , collected by P. L. Colin, CRRF, 14 November 1993; BMNH 1993.11.5.1: oceanside of Makada Reef, 15m, Duke of York Islands, East New Britain, Papua New Guinea,  $4^{\circ} 6.68'S$ ,  $152^{\circ} 23.87'E$ , collected by P. L. Colin, CRRF, 5 November 1993; BMNH 1993.10.29.1: overhang on outer reef near Albatross Passage, 6-12m, north-western New Ireland, Papua New Guinea,  $2^{\circ} 45.23'S$ ,  $150^{\circ} 43.24'E$ , collected by P. L. Colin, CRRF, 29 October 1993; BMNH 1993.11.1.1: south coast wall near east end of Djaul Island, western New Ireland, Papua New Guinea,  $2^{\circ} 58.69'S$ ,  $150^{\circ} 59.33'E$ , collected by P. L. Colin, CRRF, 1 November 1993.

**DESCRIPTION**

Ramose, each branch 1-2cm diameter, approximately 30cm length, branches anastomosing, forming large clumps hanging off overhangs or growing erect from coral surface (Fig. 5H). Texture, slightly compressible, difficult to tear, rubbery. Surface, conulose but microscopically smooth. Colour in life cream flecked with garnet-brown (9D7) and copper red (7C7), tips and undersides pale cream. Ostia, set in garnet

brown stellate surface depressions, set in a paler copper red surrounding.

**Skeleton.** Primary fibres, 300-600 $\mu$ m diameter, run parallel with branch, connected by perpendicular short secondary fibres, 120-300 $\mu$ m diameter (Fig. 6F). Dendritic fibres, 30-50 $\mu$ m diameter, radiate from tip of primary fibre, occasionally branching, forming surface brushes. Interstitial megascleres, abundant in choanosome. Ectosome, 300-450 $\mu$ m deep on sides of branches. Larger category of spinorhabds distributed in an ordered layer just below surface of sponge, abundant in choanosome and along ectosome-choanosome boundary in places (Fig. 6F).



*Spicules. Megascleres.* Subtylostrongyles: 274(250-320) x 2.5-8µm, n=30.

*Microscleres.* Spinorhabd I: spines are relatively regular in shape, disposed in four equidistant, frequently incomplete whorls: 39(33-48) x 2.4µm (Fig. 7F). Spinorhabd II: sharp conical spines of equal length, disposed in regular whorls along shaft, each equidistant from the other: 58(46-67)µm, n=10, total maximum width 14-26µm, shaft diameter 5-10µm (Fig. 8D).

#### GEOGRAPHIC DISTRIBUTION

Bismarck Sea (Fig. 4B), very common on barrier patch reefs of western New Ireland, New Britain, and Madang, north coast of mainland Papua New Guinea, particularly common around Djaul Island off the northwest tip of New Ireland (L. J. Bell, pers. comm. 1994).

#### SUBSTRATE, DEPTH RANGE, ECOLOGY

Found predominantly on ledges, overhangs, on cave walls within 10 to 30m. Reproduction by production of large yellow-pigmented larvae.

#### ETYMOLOGY

For the Bismarck Sea.

#### REMARKS

General morphology, growth form, and colouration of this northern Papua New Guinean species is remarkably similar to that of *Diacarnus ardoukoba* from the Gulf of Aden. Both are ramose, have a relatively thin ectosome, and possess a second larger category of spinorhabd disposed in a central to upper ectosomal layer and throughout the choanosome. The major difference between these two species is the spicule size and morphology of the largest spinorhabds. Megascleres and microscleres in *D. bismarckensis* are longer than in *D. ardoukoba*, and the latter are more abundant in *D. bismarckensis*. In *D. bismarckensis*, microsclere spines are very regular, of equal length, and disposed equidistantly along the shaft of the spicule. In *D. ardoukoba*, spines are irregular, with the central whorl of spines being longer, and disposed closer to the ends of the spinorhabd. These differences are also apparent in the smaller spinorhabds of *D. ardoukoba*.

#### *Diacarnus tubifera* sp. nov. (Figs 4B, 5I, 5J, 6G, 7G, 8E)

#### MATERIAL EXAMINED

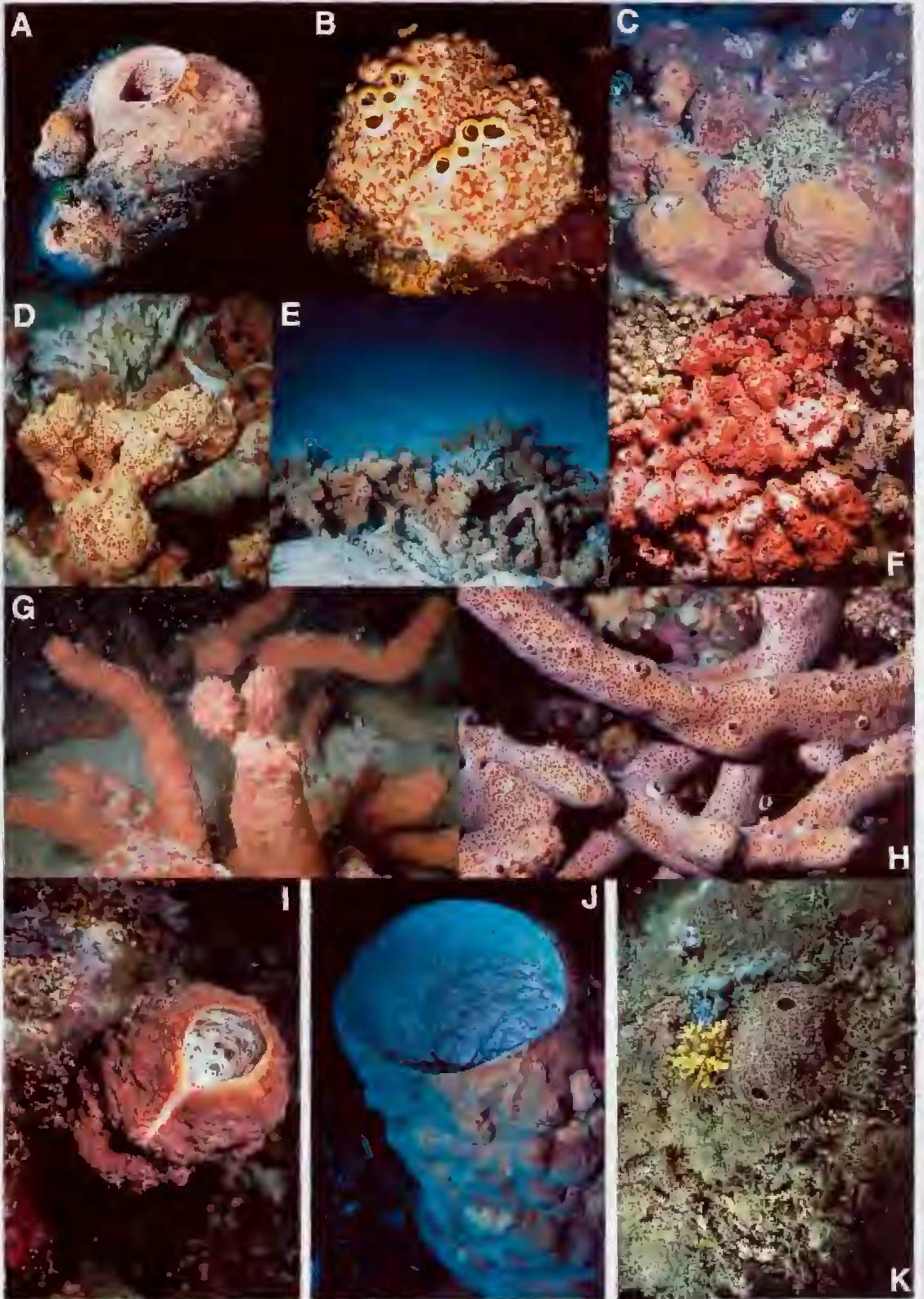
**HOLOTYPE:** QMG305012: oceanside reef near Pizion Island, Chuuk Atoll, Micronesia, 45m, 7° 11.10'N, 151° 50.20'E, collected by P. L. Colin, CRRF, 7 January 1994; **FRAGMENT OF HOLOTYPE:** BMNH 1994.5.22.2

**ADDITIONAL MATERIAL:** BMNH 1994.5.22.1: west side of East Fayu Island, 30.5m, 60nautical miles north-northwest of Chuuk Atoll, Micronesia, 8° 47.15'S, 151° 20.01'E, collected by P. L. Colin, CRRF, 14 January 1994; BMNH 1994.5.22.10 (fragment of OCDN 716-M): west side of barrier reef surrounding Bagabag Island, 28m, 30nautical miles offshore on northern Papua New Guinea coastline, 4° 32.61'N, 151° 20.01'E, collected by P. L. Colin, CRRF, 9 November 1993; Q66C-6138: attached to vertical wall, 40m, "The Grotto", southeast Watom Island, off western coast of New Britain, Papua New Guinea, 4° 6.2'S, 152° 5.7'E, collected by M. Kelly-Borges, 16 October 1991; BMNH 1993.11.1.2: south coast wall near east end of Djaul Island, western New Ireland, Papua New Guinea, 2° 58.69'S, 150° 59.33'E, collected by P. L. Colin, CRRF, 1 November 1993.; BMNH 1993.10.22.1: oceanside of Eastern Fields Atoll, 9m, Coral Sea, 90 miles southwest of Port Moresby, southern Papua New Guinea, 10° 00.80'S, 145° 40.24'E, collected by P. L. Colin, CRRF, 22 October 1993; BMNH 1995.7.4.5: Tubbataha Reefs, south of Cagayan Islands, Sulu Sea, Philippines, 8°40'N, 120°E, disturbed rubble and sand, 10m, collected by L. Sharron, 21 April 1995; BMNH 1995.7.4.3: Tubbataha Reefs, south of Cagayan Islands, Sulu Sea, Philippines, 8°40'N, 120°E, on vertical coral wall, 37m, collected by L. Sharron, 22 April 1995; BMNH 1995.7.4.2: Puerto Princessa, Palawan, Philippines, 9°50'N, 118°30'E, 12-18m, collected by P.L. Colin, 15 April 1995.

#### DESCRIPTION

Single tubular to vase-shaped, very heavy, thick-walled (Fig. 5I), average height 80cm, 15-30cm wide, most frequently twice as tall as wide, with large lobate processes on the outer surface, surface tuberculate. Atrium, apical, typically up to 15cm wide in vase-shaped sponges (Fig. 5J), typically about 8cm diameter in tubular sponges. Smaller specimens extremely conulose, often 10-14cm diameter, 9-10cm high, with a 5cm wide atrium. Texture, very firm, rubbery, mesohyl matrix very dense, fleshy. Colour in life carrot red (6B7) mottled with bright reddish brown (9D8), very patchy, interior of tube bright white, beige in ethanol.

*Skeleton.* Primary fibres, 450-600µm diameter, sparse, run longitudinally, anastomosing along axis of tubular body towards sponge apex. Large





branches, 150-300µm diameter, emerge some distance below ectosome-choanosomal boundary from upper 5-10mm of primary fibre. Fibre extensions radiate towards sponge surface, branching many times before entering ectosome (900-2400µm deep; average depth 1500µm, with lacunae 30-60µm wide), forming an immense number of very fine, long, dendritic fibres which meander through choanosome and ectosome ultimately forming small surface brushes in outer ectosome (Fig. 6G). Immense umbells raise surface into rounded lobes. Abundant megascleres form a palisade superimposed over the surface brushes. Primary fibres anastomose, also connected by short secondary fibres 120-300µm diameter. Interstitial megascleres, abundant, arranged in loose broad bundles between primary fibres. Large spinorhabds, scattered in outer ectosome, slightly more abundant in outer third of ectosome, absent from outer 50µm, common throughout choanosome. Megascleres and microscleres abundance variable between specimens. Smaller category of spinorhabds dispersed under ectosome-choanosome boundary.

*Spicules.* *Megascleres.* Subtylostrongyles: 304(250-345) x 2.5-5µm, n=30.

*Microscleres.* Spinorhabd I: extremely fine with fine spines dispersed along shaft: 38(38-41) x 2.5µm, n=10 (Fig. 7G); Spinorhabd II: distinct whorls of spines: 60(55-67) x maximum width 17-19µm, shaft width 3.5-5µm, n=30 (Fig. 8E).

#### GEOGRAPHIC DISTRIBUTION

Chuuk Atoll and East Fayu Island, Micronesia; Bismarck Sea, widely and sparsely distributed on barrier patch reefs of western New Ireland and New Britain, and Madang on northern coast of mainland Papua New Guinea (L. J. Bell, pers. comm.); Eastern Fields Atoll, southern Papua New Guinea (Fig. 4B).

#### SUBSTRATE, DEPTH RANGE, ECOLOGY

Solitary and uncommon in any one locality, they are found on vertical walls and steep-sloped oceanic fringing reefs to depths of 45m. Mode of

reproduction not observed, sponge surface frequently completely infested with barnacles.

#### ETYMOLOGY

Reflects the consistently tubular morphology.

#### REMARKS

*Diacarnus tubifera* is conspicuous and easily recognised in the field as large long solitary or double tubes, with an extremely heavy, rubbery texture. Smaller specimens are also tube-shaped and extremely conulose, also with a deep central atrium. Histologically, the sponge is well differentiated from all species described thus far. The sponge has a very thick ectosome which is ramified with abundant dendritic fibres which emanate well within the choanosome, arising to form a lobed surface. The megascleres and large category of spinorhabds are larger than in previously described species, and the large spinorhabds are scattered throughout the ectosome rather than being restricted to a distinct mid-ectosomal band such as in *D. ardoukoba* and *D. bismarckensis*.

#### *Diacarnus megaspinothabdosia* sp. nov.

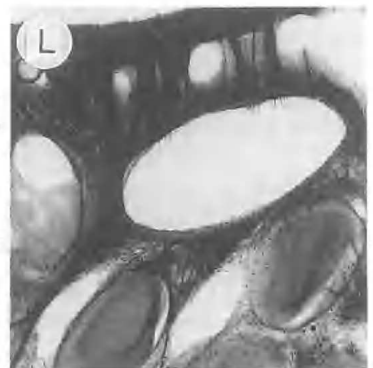
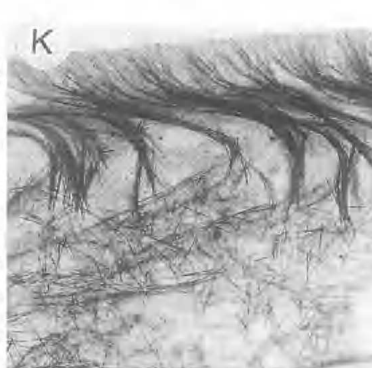
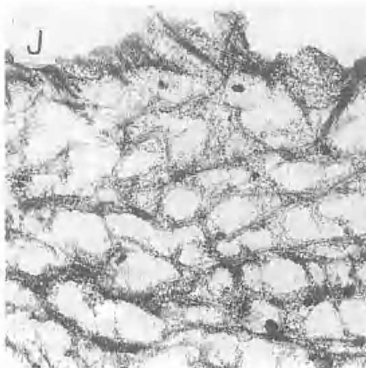
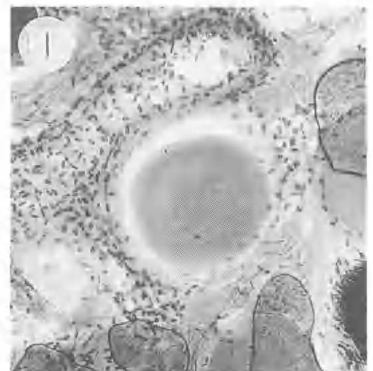
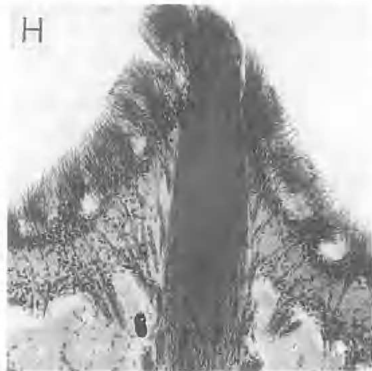
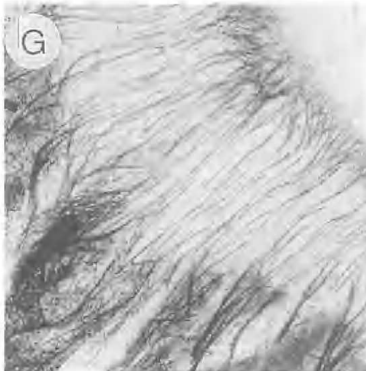
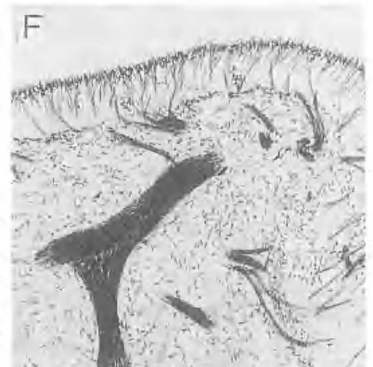
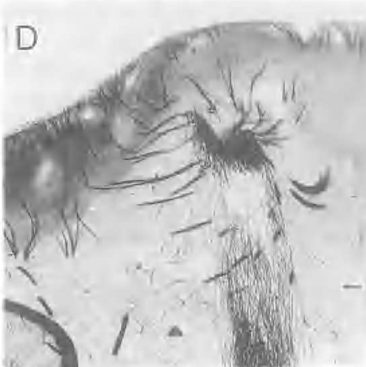
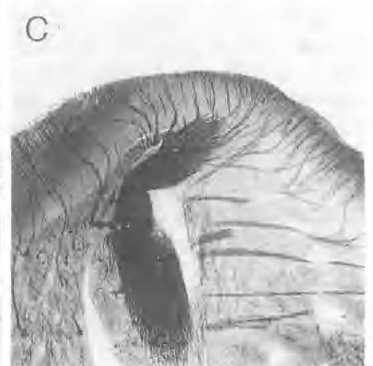
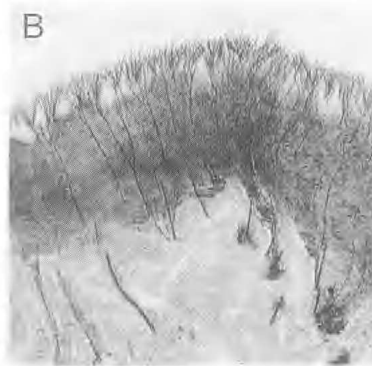
(Figs 4B, 5K, 6H, 6I, 7H, 8F)

#### MATERIAL EXAMINED

HOLOTYPE: QMG305013: fringing reef 150m south of Motupore Island, 10m, Bootless Bay, Papua New Guinea, 9° 31.6'S, 147° 16.6'E, collected by M. Kelly-Borges, 6 December 1985; FRAGMENTS OF HOLOTYPE: BMNH 1994.5.22.6, NSRC(UPNG) 90.

ADDITIONAL MATERIAL: BMNH 1994.5.22.5: (fragment of OCDN 673-P): lagoon side of Tab (Pig) Island, 10m, on Madang barrier reef, Papua New Guinea, 5° 10.21'S, 145° 50.37'E, collected by P. L. Colin, CRRF, 3 November 1992; HBOM 003:00925: fringing reef south of Motupore Island, 10m, Bootless Bay, Papua New Guinea, 9° 31.6'S, 147° 16.6'E, collected by M. Kelly-Borges, 24 January 1994; BMNH 1994.7.25.1 (fragment of OCDN 2693-M): attached to rubble, 7m, Gamao Point, Batangas, Philippines, 13° 38.39'N, 120° 56.86'E, collected by C. Arneson, CRRF, 25 July 1994; BMNH 1995.5.7.4.1: Zambales, West Luzon, Philippines, 15°50'N, 120°E, silty reef, 18m, collected by P. L. Colin, 2 May 1995; BMNH 1995.7.4.4: Zambales, West Luzon, Philippines, 15°50'N, 120°E,

FIG. 5. Species of *Diacarnus* *in situ*. See descriptions in text for size in life. A. *Diacarnus spinipoculum* (Carter), Fiji, BMNH 1994.8.20.1. B-C. *Diacarnus bellae* sp. nov., Chuuk Atoll, Micronesia: B. solitary form, BMNH 1994.5.22.9. C. coeulescent form, holotype QMG305007. D-E. *Diacarnus erythraenus* sp. nov., Djeddah, Red Sea, holotype QMG305008. F. *Diacarnus levii* sp. nov., Belep, New Caledonia, holotype QMG305009. G. *Diacarnus ardoukoba* sp. nov., Djibouti, holotype QMG305010. H. *Diacarnus bismarckensis* sp. nov., Djaul Island, Papua New Guinea, BMNH 1993.11.1.1. I-J. *Diacarnus tubifera* sp. nov., Djaul Island, Papua New Guinea: I. tubular form, BMNH 1993.11.1.2; J. vase-form. K. *Diacarnus megaspinothabdosia* sp. nov., Batangas, Philippines, BMNH 1994.7.25.1.





43m, collected by P.L. Colin, 3 May 1995; BMNH 1995.9.1.1, BMNH 1995.9.1.2; south side of Puerto Princessa Bay, Puerto Princessa, Pallangbato, Philippines, 9°41.62'N, 118°4.51'E. Collected by P.L. Colin CRRF, 15 April 1995.

#### DESCRIPTION

Thickly encrusting, lobate, some specimens with restricted base of attachment, 6-15cm diameter, lobes up to 4cm high (Fig. 5K). Lobe apices covered in tough sharp conules approximately 2 mm high, 2-5mm apart. Oscules, 1-3mm diameter, with smooth raised cream collars, scattered apically on lobes or irregularly over surface. Texture, barely compressible, tough, harsh to touch but microscopically velvety between conules. Colour in life oxblood red (9E8), mustard (5C8) internally, uniformly cream (4A2) in ethanol. BMNH 1994.5.22.5 from Madang was pale brown (4B4) in life due to shading effects. Very large bright yellow embryos are abundant in BMNH 1994.5.22.6 (Fig. 6I).

**Skeleton.** Primary fibres, sparse, tough, up to 900µm diameter, raise surface into well-separated tough, sharply pointed conules (Fig. 6H). Primary fibres joined by short, very thick, secondary fibres, up to 500µm thick. Sparse spicule tracts, 60-100µm wide, diverge from primary fibre well within choanosome, branching, occasionally forming well separated tracts that radiate within ectosome. Tracts end in dense brushes at surface where they interdigitate with a dense loose palisade of megascleres. Interstitial megascleres, numerous in choanosome, dispersed without order between fibres. Larger fibres are surrounded by a sheath of bundles of collagen fibrils, 60-80µm thick, which also contains loose megascleres arranged longitudinally along fibre. Large spinorhabds, abundant in ectosome and disposed in an undulating band in upper portion of ectosome surrounding lacunae, also abundant above lower ectosomal boundary and abundant in choanosome, sometimes patchily, sometimes concentrated around canals (see Fig. 6I). Small spinorhabds, below ectosomal-choanosomal boundary.

**Spicules.** *Megascleres.* Subtylostrogyles; 318(298-346) x 7-12µm, approximately 20µm shorter (average) in BMNH 1994.5.22.5 from Madang.

*Microscleres.* Spinorhabds I: slender rods with regular whorls of small spines; 48(43-55) x 3-5µm, shaft 1µm wide (Fig. 7H); Spinorhabds II: spines blunt, central shaft very thick, occasionally malformed with central shaft bare or spines re-curved along shaft; 84(74-96)µm, n=30, maximum width 36(34-48), shaft width: 15(10-19)µm (Fig. 8F).

#### SUBSTRATE, DEPTH RANGE, ECOLOGY

Found on silty, fringing coral reefs down to 10m. Choanosome contains large conspicuous embryos of parenchymella type, up to 1.5mm diameter. Easily observed in specimens in the field, they are bright orange-yellow, contrasting with cream mesohyal matrix, they are abundant, present at any time of collection. Larvae, loosely embedded within the central part of body (Fig. 6I), many contain thin megascleres dispersed without order in central region. Microscleres, absent from embryos. Round or ovoid inclusions, 50-80µm diameter, with a fibrillar content, abundant in the choanosome, possibly spermatocysts.

#### GEOGRAPHIC DISTRIBUTION

Northern (Madang), southern (Motupore Island) Papua New Guinea; Batangas, Philippines (Fig. 4B)

#### ETYMOLOGY

Reflects large size and abundance of largest category of spinorhabds.

#### REMARKS

The major character separating *Diacarnus megaspinothabdosus* from other species of *Diacarnus* is the possession of extremely large spinorhabds, and the largest average megasclere dimensions. These microscleres form dense aggregations in the choanosome and are disposed in an upper and lower layer within the ectosome.

FIG. 6. A-L, Skeletal arrangements of *Diacarnus* and *Negombata* spp. A, *Diacarnus spinipoculum* (Carter), holotype BMNH 1846.10.14.174, 30 x. B, *Diacarnus bellae* sp. nov., BMNH 1994.5.22.11, 30 x. C, *Diacarnus erythraeanus* sp. nov., MNHN DJV52, 30 x. D, *Diacarnus levii* sp. nov., holotype QMG305009, 30 x. E, *Diacarnus ardoukoba* sp. nov., holotype QMG305010, 30 x. F, *Diacarnus bismarckensis* sp. nov., BMNH 1994.5.22.12, 30 x. G, *Diacarnus tubifera* sp. nov., BMNH 1994.5.22.10, 30 x. H-I, *Diacarnus megaspinothabdosus* sp. nov., holotype QMG305013. H, skeletal arrangement, 30 x. I, larva, 120 x. J, *Negombata corticata* (Carter), holotype BMNH 1840.5.6.56-58, 30 x. K-L, *Negombata magnifica* (Keller): holotype fragment BMNH 1908.9.24.118, 30 x. L, MNHN DJV56, 120 x.

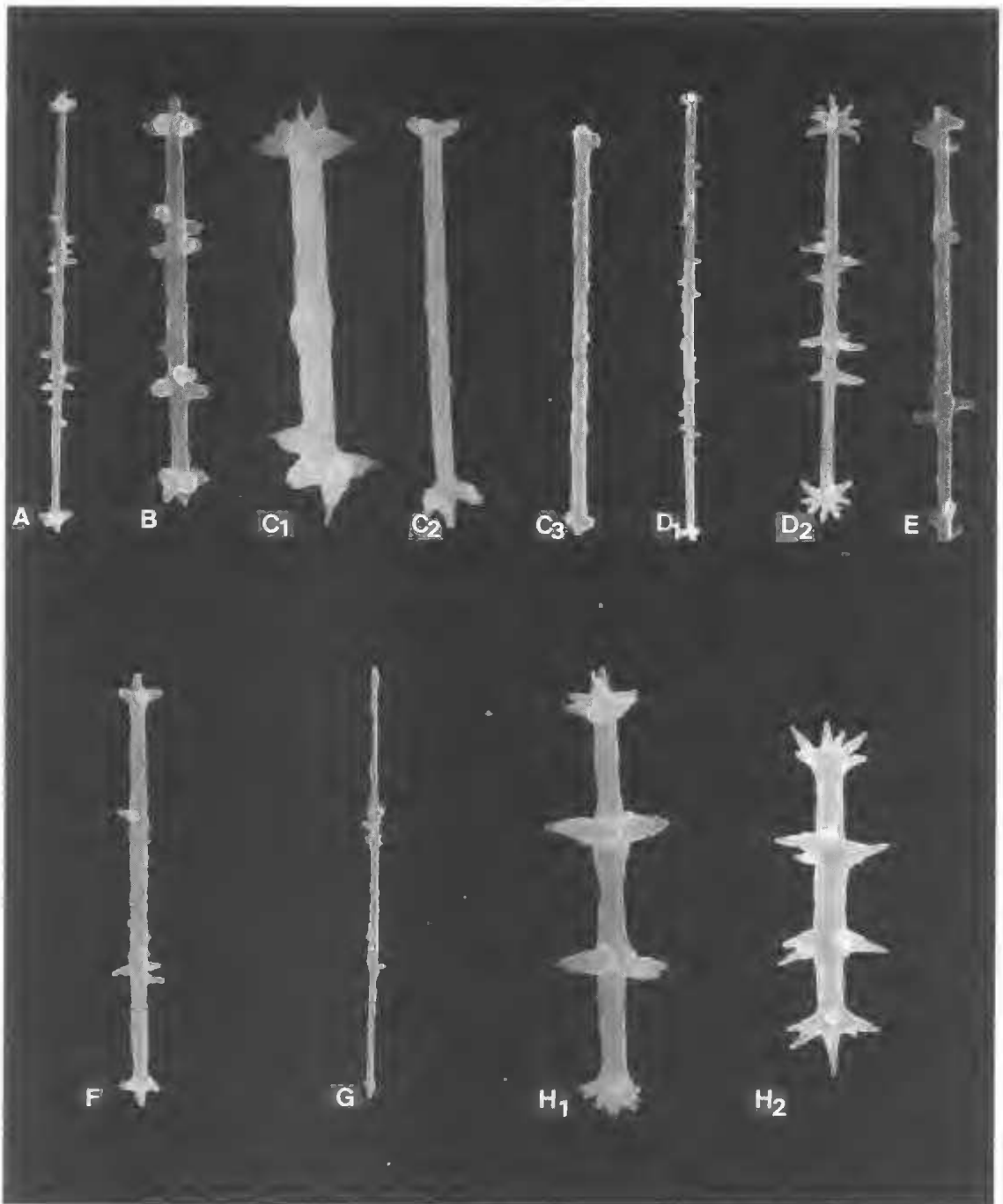


FIG. 7. A-H, Scanning electron micrographs of spinorhabd I microscleres of *Diacarnus* spp. A, *Diacarnus spinipoculum* (Carter), holotype BMNH 1846.10.14.174. Scale: 21.2 $\mu$ m. B, *Diacarnus bellae* sp. nov., BMNH 1994.5.22.11. Scale: 18.5 $\mu$ m. C, *Diacarnus erythraeanus* sp. nov., MNHN DJV52, Red Sea. Scale: C1: 12.6 $\mu$ m; C2, C3: 9.1 $\mu$ m. D, *Diacarnus levii* sp. nov., D1 = holotype QMG305009, D2 = BMNH 1994.5.22.8. Scale: 21.1 $\mu$ m. E, *Diacarnus ardoukoba* sp. nov., holotype QMG305010. Scale: 9.3 $\mu$ m. F, *Diacarnus bismarckensis* sp. nov., holotype QMG305011. Scale: 13 $\mu$ m. G, *Diacarnus tubifera* sp. nov., BMNH 1994.5.22.10. Scale: 15.1 $\mu$ m. H, *Diacarnus megaspinothabdos*a sp. nov., holotype QMG305013. Scale: H1: 16.2 $\mu$ m; H2: 28 $\mu$ m.

**Negombata de Laubenfels***Negombata* de Laubenfels, 1936: 159

## TYPE SPECIES

*Latrunculia corticata* Carter, 1879: 298 (by subsequent designation, de Laubenfels, 1936: 159)

## DIAGNOSIS

Erect, massive, lobate to elongate, finger-forming, branching. Compressible, with an extremely smooth surface through which large pores are clearly visible. Megasclere skeleton consists of a uniform, elongate, to square-meshed reticulation of clear spongin cored fairly irregularly with thick, slightly curved oxea with strongylote ends, and a clear hollow axial canal. Ectosome, with thin fusiform wavy oxeas in tracts that fan within a thick collagenous ectosome, ultimately forming surface brushes. Microscleres, irregular spinorhabds in two sizes, largest very irregular, thick, without a distinct shaft, smaller, with a distinct straight or curved shaft with spines of uneven length arranged roughly in two central whorls and two terminal bunches, terminal spines commonly double. Immature microscleres, straight rods in which one or more spines from apices are strongly recurved, disposed predominantly on very outside of ectosome, but can also be very dense within choanosome.

*Negombata corticata* (Carter)  
(Figs 2, 6J)*Latrunculia corticata* Carter, 1879: 298; Keller, 1889: 401

## MATERIAL EXAMINED

HOLOTYPE: *Latrunculia corticata* BMNH 1840.5.6.56-58: "from the Red Sea", three dried fragments from the same specimen (Fig. 2).

## DESCRIPTION

Carter (1879) described the sponge as being "erect, solid, lobate...apparently subsessile". Type specimen consists of short, ridged, broad fans of different lengths with a restricted base of attachment (Fig. 2). Colour, yellowish white in dry sponge. Surface texture of dry holotype, fibrous, roughened due to shrinkage. Carter (1879) described the fresh sponge as "chondroid" and "smooth as varnish to the unassisted eye" with pores 20µm diameter and 74µm apart.

*Skeleton.* Reconstitution of the dry holotype allowed examination of the skeletal organization

of this sponge. The skeleton consists of a central axis of rectangular meshes formed by spongin fibres, 300-600µm diameter, not clearly differentiated into primary and secondaries (Fig. 6J). Large oxea are embedded within the fibres, and also occur interstitially. Megascleres are not arranged uniformly within fibres, but rather, are scattered singly or in groups, and oblique or occasionally perpendicular to fibre axis. An ectosomal skeleton of wavy oxea is present, but this has collapsed in the holotype, rendering the arrangement difficult to determine. Microscleres, densely packed on sponge surface and also in choanosome, almost obscuring choanosomal fibres.

*Spicules. Megascleres.* I. Oxeas of main fibroreticulation: thick, straight or slightly curved with rounded strongylote ends, centrally thickened with a distinct hollow axial canal: 346(317-384) x 10-12µm, n=30; II. Ectosomal oxea: thin, fusiform irregularly curved, wavy, disposed in surface plumose brushes: 422(394-451) x 2.4-6µm, n=30.

*Microscleres.* I: Irregular, shaft rarely distinct, overall shape of microsclere straight, curved slightly or spiralled, spines of uneven length arranged roughly in two central whorls and two terminal bunches, terminal spines commonly double: 26(19-31)µm, n=30; maximum width 14-19µm, shaft width 3-6µm, n=10; II: Extremely irregular spinorhabds, almost oval when heavily centrally thickened, shaft indistinct and spines unevenly distributed along sides of the spicule: 35(26-43)µm, n=30, maximum width 17-24µm, shaft width 7-10µm, n=10.

## SUBSTRATE, DEPTH RANGE, ECOLOGY

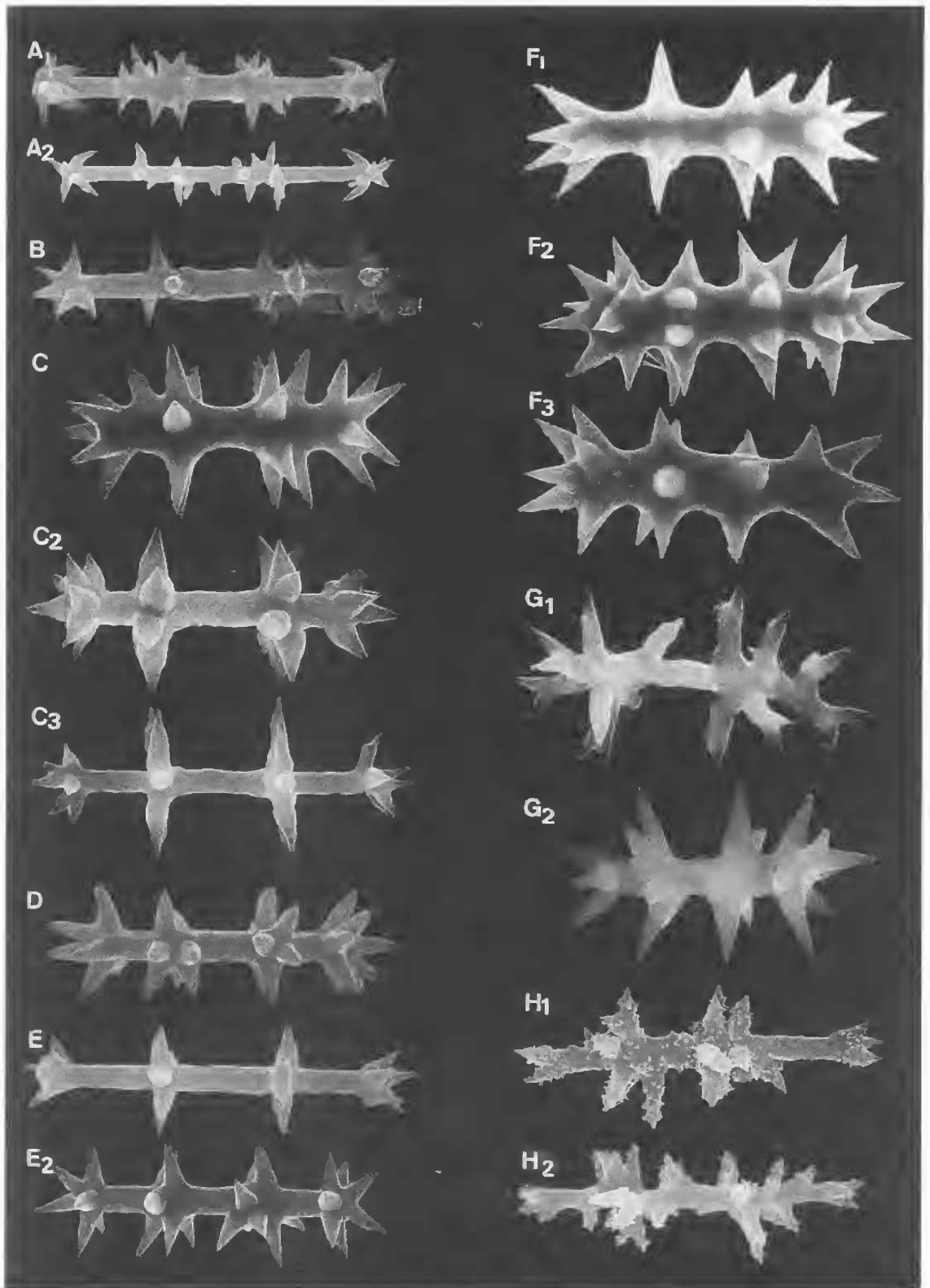
There is no information given in Carter (1879) on the ecology or habitat of this species.

## GEOGRAPHIC DISTRIBUTION

Carter (1879) noted that the sponge was supplied by a dealer who stated that the sponge came from the Red Sea.

## REMARKS

Examination of a spicule preparation of the holotype of *Latrunculia corticata* Carter (BMNH 1840.5.6.56-58) indicates that this sponge differs considerably from species recognised within *Diacarnus* s.s., *Sigmosceptrella* s.s., or *Latrunculia* s.s. The megascleres of *Negombata* are two forms of wavy oxea, instead of subtylostrongyles as in *Diacarnus* and styles in *Latrunculia*. Examination of the reconstituted





skeleton of the type specimen reveals megascleres embedded in spongin forming a rectangular mesh from which short ectosomal tracts of thinner, wavy oxeas arise to form plumose brushes within the ectosome. In *Diacarnus* the fibres are clearly differentiated into very large primary fibres, with smaller secondary fibres giving rise to dendritic tertiary fibres in a plumose umbelliform arrangement. Although the microscleres of *Negombata* are also spinulate, they differ from those of other latrunculiid genera. The largest category are so irregular they look like spined lumps of silica, the smaller category are also irregular with dense, frequently double terminal spines that are arranged only vaguely in whorls. The overall spicule is frequently curved or spiralled, with a distinct shaft only rarely visible. The smaller category of spinorhabds derive from straight rods in which one or more spines from the apices are strongly recurved. Carter's illustrations of regular microscleres are thus misleading.

*Latrunculia purpurea* Carter, from Bass Strait, southern Australia, was also regarded by de Laubenfels (1936) to be a species of *Negombata*. However, *Latrunculia purpurea* appears to be a valid species of *Latrunculia*. Carter (1881) described a "flat, compressed, circular, thin, cake-like or fungiform" sponge, brown-purple in colour, with a "ragged and proliferous upper surface". There is no mention, however, of a "chondroid dermal region" and "fibroreticulate internal structure" described for *Negombata corticata*, rather, the internal structure is "compact and densely spiculous." The microscleres of *Latrunculia purpurea* are typical of *Latrunculia* as the two inner spined discs are disposed towards one end of the spicule, and the microscleres are disposed "to the circumference on the upperside and darker portions, arranged perpendicularly in juxtaposition with the spinous disk of one end outwards (Carter, 1881)." The megascleres, however, are described and illustrated as being oxeote as in *Negombata corticata* and unlike the polytote or uniform styles of *Latrunculia*. However,

without examination of the type material, it is impossible to speculate further on the affiliations of this specimen.

De Laubenfels (1936) also considered the possibility that *Negombata* was synonymous with *Negombo* Dendy. It is clear from examination of the type species *Negombo tenuistellata* Dendy (BMNH 1907.2.1.28) that this is not the case; the megascleres of *Negombo tenuistellata* are gently curved large styles arranged in vague longitudinal to reticulated tracts within thin hollow-walled tubes, and the microscleres are different, as already shown (see remarks for *Diacarnus spinipoculum*).

***Negombata magnifica* (Keller)**  
(Figs 3K, 3L, 4C, 6K, 6L, 8G)

*Latrunculia magnifica* Keller, 1889: 402

**MATERIAL EXAMINED**

FRAGMENT OF HOLOTYPE: *Latrunculia magnifica* BMNH 1908.9.24.118 (fragment from the Berlin Museum) from Suakin, Sudan, Red Sea.

ADDITIONAL MATERIAL: MNHN DJV56: Musha Island, Djibouti, 24m, 11°42.50'N, 43°08.45'E, collected by J. Vacelet, 23 January 1985 (M 3), (fragment deposited as BMNH 1994.5.22.18)

**DESCRIPTION**

Keller (1889) described the sponge as having many long cylindrical digits arising from a short spreading stalk. A specimen 30cm high, was described as having 25 branches of equal length with a uniform diameter of 6-10mm. Although the digits do not commonly divide to form branches, occasional short stumps or incipient branches are seen. The texture was described as compressible but firm and elastic. The surface of the sponge was completely smooth, slightly shiny, with a translucent surface, and punctured with regularly spaced pores 100-150µm diameter. Oscules were uncommon, tear-shaped and raised slightly on collars. The colour in life was described as deep red-orange which remained in the preserved specimen for a considerable time

FIG. 8. Scanning electron micrographs of spinorhabd II microscleres of *Diacarnus* spp., *Negombata magnifica* (Keller), and acanthose microrhabds of *Negombo tenuistellata* Dendy: A, *Diacarnus spinipoculum* (Carter), holotype BMNH 1846.10.14.174. Scale: A1: 24.2µm; A2: 28.2µm. B, *Diacarnus bellae* sp. nov., BMNH 1994.5.22.11. Scale: 18.2µm. C, *Diacarnus ardukobae* sp. nov., holotype QMG305010. Scale: C1: 21.3; C2: 16.6µm; C3: 14.6µm. D, *Diacarnus bismarckensis* sp. nov., holotype QMG305011. Scale: 21.3µm. E, *Diacarnus tubifera* sp. nov., BMNH 1994.5.22.10. Scale: E1: 18.2µm; E2: 24.2µm. F, *Diacarnus megaspinorhabdosa* sp. nov. holotype QMG305013. Scale: F1: 34µm; F2: 30.3µm; F3: 34µm. G, *Negombata magnifica* (Keller) MNHN DJV 56. Scale: G1: 9.1µm; G2: 12.5µm. H, *Negombo tenuistellata* Dendy 1905, holotype BMNH 1907.2.1.28, acanthose microrhabd microscleres. Scale: 5.2µm.

before eventually fading. The ectosome was more intensely coloured than the interior of the sponge. Embryos of the parenchymella type were present and large (825-1125µm diameter).

**Skeleton.** Details of gross morphology, histology, arrangement of the choanosomal skeleton, and spiculation were accurately described and illustrated by Keller (1889). However, for consistency these are re-interpreted here with details of the ectosomal skeleton not evident in the holotype *Negombata corticata*. The skeleton consists of a central axis of thick strongylote oxeas bound into an irregular round-meshed reticulation with abundant stratified spongin. Interstitial megascleres are common. Primary fibres cannot be clearly distinguished from secondary fibres which average 125µm diameter (range: 60-300µm). Keller (1889) notes and illustrates the presence of a "parasitic" algae, thought to be a species of *Calithamilton*, living within the spongin fibres. This was not observed in any of our specimens. A distinct ectosomal skeleton is present and consists of regularly and closely spaced compact spicule tracts 30-70µm wide which divide and diverge towards the ectosome where they form fanned brushes (Fig. 6K). Megascleres of the ectosomal skeleton are wavy fusiform oxeas rather than the shorter thicker strongylote oxea embedded in the spongin fibre. The tips of these spicules protrude through the dermal membrane in patches. Microscleres are common within the choanosome and present as a distinct layer in the upper third of the ectosome. The ectosome is distinct, collagenous, approximately 180µm deep (range 240-430µm), and perforated by vertical poral canals 150-200µm wide which lead to subdermal lacunae.

**Spicules. Megascleres.** I: Oxeas of main fibro-reticulation, thick with hollow central axis, straight or slightly curved, with slightly restricted strongylote ends: 346 (298-385) x 10(4.8-12)µm, n=30; II: Ectosomal oxea, fusiform irregularly curved, wavy, disposed in surface plumose brushes: 435 (403-490) x 1-3µm, n=30.

**Microscleres.** I. Slender, straight, curved slightly or spiralled, spines of even length and arranged in two discrete central whorls with terminal bunches, terminal spines commonly double, occasionally recurved, shaft clearly distinguished between spines: 23(19-26)µm, n=30; maximum width 10-12µm, shaft width 3µm, n=10 (Fig. 3K, 3L); II: Spicule very stout with short scattered irregular spines, spines absent in some parts of the microsclere: 33(24-

41)µm, n=30; maximum width 22-26µm, shaft width 7-20µm, n=10 (Fig. 8G).

#### SUBSTRATE, DEPTH RANGE, ECOLOGY

The sponge was abundant on coral reefs and vertical coral walls, and is one of the most prominent sponges in the Gulf of Eilat between depths of 3-30m (Kashman et al., 1980). Very large embryos were abundant in a sponge collected in July of 1985 (Fig. 6L). It is not known whether these are pigmented bright yellow-orange as in *Diacarnus*.

#### GEOGRAPHIC DISTRIBUTION

Suâkin, Sudan, Red Sea; Djibouti, Gulf of Aden (Fig. 4C)

#### REMARKS

*Negombata magnifica* is distinct from *N. corticata* in gross morphology, *N. magnifica* forming long, cylindrical, whip-like branches, the later being a clump of broad ridged fans. Histologically, the species are rather similar, but with discernable dimensional and morphological differences between the megascleres and microscleres. The later are extremely dense in the choanosome of *N. corticata*. The spongin skeleton of *N. corticata* is more robust.

#### DISCUSSION

*Diacarnus* and *Negombata* are distinct within the Latrunculidae as they possess a fibro-reticulate skeleton with an unusual umbelliform "ectosomal" skeleton developed to a greater or lesser degree, and a highly collagenous mesohyl matrix structure with tough fibres which superficially resemble vertebrate ligaments in soft tissue. *Diacarnus* is remarkably homogenous with the skeletal arrangement, huge fibres and spicule dimensions of all species being similar. We have emphasised the gross morphology of the sponge, coupled with the presence or absence of a second larger category of microsclere, and the morphology of these spicules, in recognizing new species. The disposition of these microscleres throughout the sponge, and spicule and fibre dimensions are less reliable characters for species differentiation. *Diacarnus spinipoculum* and *D. tubifera* are both vasiform but the former is barrel-shaped rather than tubular. These two species are further separated on the presence of large spinorhabds in *D. tubifera*, in addition to very abundant dendritic tertiary spicule tracts which arise from well within the choanosome of this species. *Diacarnus*

*bellae* from Micronesia and *D. levii* from New Caledonia are very similar but are separated on gross morphology and spicule dimensions. The three ramose species *D. erythraeanus*, *D. ardoukoba*, and *D. bismarckensis*, are separated geographically, and the two Red Sea species are further separated by the presence of large spinorhabds in *D. ardoukoba*. *Diacarnus megaspinorhabdosa* has the largest megascleres of all species thus far described, and highly diagnostic spinorhabds.

Although there are many similarities between *Negombata* and *Diacarnus*, there are several major differences which separate them, including the presence of diactinal megascleres and a regular tight-meshed "axial" fibrous skeleton in which the fibres are only lightly cored by megascleres. The skeletal arrangement of *Negombata* superficially resembles that of several myxillid, raspailid and microcionid pocilosclerid genera which emphasise an axial fibroreticulation and ectosomal brush-forming skeleton. In *Diacarnus*, the fibres are packed regularly with spicules with no visible spongin surrounding them. *Negombata corticata* and *N. magnifica* are differentiated primarily on gross morphology, spicule differences, and possibly the development of the ectosomal skeleton.

Sponges previously identified as *Latrunculia magnifica* (Keller) from the Red Sea uniquely contain compounds known as latrunculins (Nee-man et al., 1975; Kashman et al., 1980). With the transfer of this species to *Negombata* here, the latrunculins become a potentially diagnostic chemical marker for sponges of the genus *Negombata*. Several latrunculin - containing voucher specimens from the Philippines and Indonesia supplied by M-K. Harper (Scripps Institute of Oceanography) and the Coral Reef Research Foundation, were examined as this report went to press. While these sponges are clearly related morphologically to the two known species of *Negombata*, there are considerable differences, requiring the examination of further material before a complete identification can be made. Species identified as *Latrunculia brevis* and *L. conulosa* from Australia (in Butler & Capon, 1991; 1993), *Sigmosceptrella laevis* (Albericci et al., 1982), and *Diacarnus bellae* sp. nov. (F. J. Schmitz, D. J. Faulkner, pers. comm.), contain norsesquiterpene peroxides. Confirmation of previous identifications for the specimens whose chemistry is known and has been published, is presently being carried out (Kelly-Borges and Mattern, in prep.).

The possession of large tracts of diverging megascleres, megasclere brushes at the surface, spined acanthomicrorhabds, and large bright yellow larvae, in *Diacarnus* and *Negombata*, is reminiscent of *Sigmosceptrella* Dendy. Examination of the type species of *Sigmosceptrella*, *S. quadrilobata* (BMNH 25.11.1.1641), and *Spirastrella* (= *Sigmosceptrella*) *fibrosa* Dendy (1897), which Dendy (1922) regarded as the 'true' type species of the genus *Sigmosceptrella*, reveals several characteristics which distinguish *Sigmosceptrella* from *Diacarnus* and *Negombata*.

The largest microscleres of *Sigmosceptrella* are very similar to those of *Diacarnus* and *Negombata*; but the spines of the two inner whorls of the rhabd axis are longer than those of the terminal whorls, which are more or less in the same plane as the axis of the spicule, and they are closer to the terminal whorls than they are to each other, imparting a dumbbell appearance to the spicule (Fig. 3D, 3F, G). The spinorhabds of *Diacarnus* and *Negombata* are more regular with spines of equal length in whorls that are separated equidistantly, in most species, along the axis of the spicule (Fig. 3I, J, L). In all specimens of *Sigmosceptrella* examined, these microscleres are packed in confusion in a dermal crust at the surface (Fig. 9A, B) of the sponge, rather than scattered in a band within a broad collagenous detachable ectosome, as in *Diacarnus* and *Negombata*.

The developmental stages of the spinorhabds of these three genera also differ. The rhabds of *Sigmosceptrella* are distinctly sigmoid in shape (Fig. 3D, E, G). These were illustrated by Dendy (1905: Plate 18 Figure 4c; Dendy 1921: 122) who regarded these as the major diagnostic character for *Sigmosceptrella*. These are not to be mistaken for the "true" sigmas which can also be found in the BMNH histological slide of the holotype. There were also small anchorate isochelae and tylostyles in the section and thus the lot is obviously foreign. The earliest protorhabd forms of *Sigmosceptrella* and *Negombata* are rather more similar to each other than they are to the protorhabds of *Diacarnus*, which are simply spinulate as in the mature spicule (Fig. 3H). The earliest spines of the rhabds of *Negombata* and *Sigmosceptrella* are strongly recurved spines with kinked tips which eventually become the spines along the shaft. However, where the shaft of *Sigmosceptrella* becomes sigmoid (Fig. 3B, E) (Dendy, 1921), those of *Negombata* remain straight (Fig. 3K).

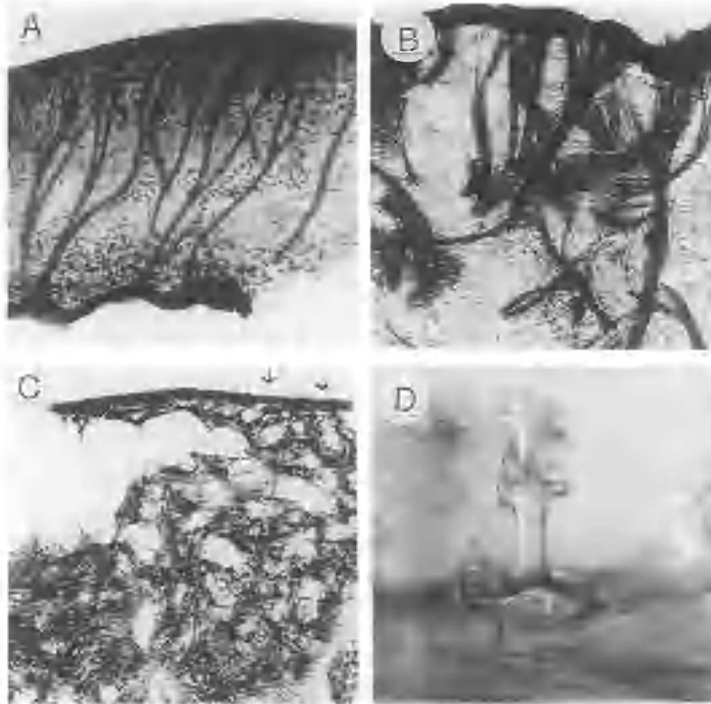


FIG. 9. A-D, Skeletal arrangements of *Sigmoseptrella* and *Latrunculia*. A, *Sigmoseptrella quadrilobata* Dendy, holotype BMNH 25.11.1.1641, Indian Ocean, 30 x. B, *Sigmoseptrella* sp., Q66C-2779, Sisters Reef, Murray Reefs, 3m, Wambro Sound near Rockingham, Perth, Western Australia, 32° 21.3'S 115° 41.3'E, 30 x. C-D, *Latrunculia* sp., Q66C-2463, Horseshoe Reef 3km WNW of Margaret Brock Lighthouse, 18m, Cape Jaffa, Kingston, South Australia, 36°56.8'S, 139°35.0'E. C, the skeleton is a wispy reticulation of loose tracts of styles, with a layer of erect discate microrhabds at surface of sponge, 30 x. D, single discorhabd with terminal spines embedded beneath the ectodermal membrane, above a layer of tangential styles, 2000 x.

The megascleres of *Sigmoseptrella* are arranged in plumose tracts which arise from the base of the sponge, branching continuously to form very fine fibres which terminate in brushes at the surface (Fig. 9A,B), unlike the plumoreticulate arrangement of huge compact spongin-bound fibres with apical umbells, as in *Diacarnus*. The fibres of *Diacarnus* are clearly visible to the unaided eye, and are separable from the mesohyl matrix, resembling ligaments. There is also no continuous dermal palisade of megascleres at the surface of *Sigmoseptrella*.

The family Latrunculiidae has an unstable history and has been switched between the orders Hadromerida (e.g., Topsent, 1922; Dendy, 1922; Bergquist, 1978), and Poecilosclerida (e.g. Lévi, 1973; Van Soest, 1984, see Hooper, 1986). As it is currently perceived, the family is heterogeneous, sharing features that belong to both orders.

*Diacarnus*, *Negombata* and *Sigmoseptrella* incubate huge parenchymella larva, and embryos 500µm of diameter have been found in a Mediterranean species of *Latrunculia* (Vacelet, 1969), while all known hadromerid sponges are oviparous. However, in contrast to the obvious affinity of these genera with poecilosclerid sponges which incubate larvae, *Diacarnus* and *Negombata*, in particular, are similar to many hadromerid genera such as *Tethya*, *Spirastrella* and *Polymastilia*, which emphasise heavily collagenous tissue, particularly in the cortex.

Although there is no clear resolution of the affinities of these genera with other demosponges, several patterns have emerged from this study of morphological characters. It is quite clear that *Diacarnus*, *Negombata* and *Sigmoseptrella* are more closely related to each other than they are to *Latrunculia*, type species of the family Latrunculiidae. The skeletons of these three genera, including another latrunculiid *Podospongia*, are in complete contrast to that of *Latrunculia*, all genera emphasising a complex plumose fibro-reticulation, while the skeleton of *Latrunculia* s.s. is a wispy reticulation of very loose

tracts of styles with a tangential surface layer of megascleres (Fig. 9C). Although the morphology of the acanthomicrorhabd microscleres in *Sigmoseptrella*, *Diacarnus*, and *Negombata* approach those of *Latrunculia* in general form, the microscleres of the latter are discate rather than spinulate. The microscleres of *Latrunculia* s.s. are arranged in a peculiar erect palisade of microscleres with their terminal disc embedded beneath the ectosomal membrane, the remainder of the microscleere free of tissue outside the sponge (Fig. 9C, D). In *Sigmoseptrella* and *Negombata*, microscleres are densely packed in the outer cortex, while in *Diacarnus* these are less dense and contained in a band mid-cortical band.

Morphological data suggest that *Latrunculia* s.s., and possibly *Barbozia* with its palmate isochelae, may be more closely related to



iophonid poecilosclerids such as *Zyzya*, as they share several features such as a tangential surface layer of megascleres, erect surface spicules (although in *Zyzya* these spicules are tangential tyloles or strongyles, and acanthoxeas, respectively), deep brown or green colouration, and in the possession of fistules. It seems likely from morphological data, also, that *Diacarnus*, *Negombata*, *Sigmosceptrella*, and *Podospongia*, should not be included in the family Latrunculiidae. Although it is clear that these genera are similar in some respects to some hadromerids (collagenous tissue, radial symmetry in *Podospongia*, etc.), the vast majority of characters are shared with poecilosclerids (plumose-reticulate fibre skeleton, chemistry, reproduction), suggesting that this group also constitutes a poecilosclerid family, but separate from the Latrunculiidae, rather than a hadromerid family. However, as there is no clear resolution of this hypothesis we retain them as *incertae sedis* within the Family Latrunculiidae until further data is available. Secondary metabolite data and DNA sequence data acquisition and analysis are currently in progress towards this end (Kelly-Borges, unpublished data).

*Diacarnus* is predominantly a shallow-water genus with a broad latitudinal distribution within tropical West Central Pacific marine environments (Fig. 4). *Diacarnus spinipoculum* is very widely and sparsely distributed in temperate south-eastern Australia and tropical Micronesia and Fiji. The longitudinal distribution is however, remarkably disjunct, as two species of *Diacarnus* also occur in the Red Sea (*D. erythraeanus* and *D. ardoukoba*) with the two known species of *Negombata*. Except in the Red Sea and Gulf of Aden, *Diacarnus* has not been recorded further west than the Philippines despite extensive recent sampling within the broad Indo-Pacific region.

This disjunct Red Sea-Indo-Pacific distribution has been indicated for several Indo-Pacific species of sponge, including well known species such as *Psammoplysilla purpurea*, *Hyrtios erecta*, *Dysidea herbacea*, *Phyllospongia papyracea*, and *Theonella swinhoei*. Sixty per cent of the Red Sea records in Lévi (1958) were of species known previously only in the Indo-Pacific. A number of Red Sea coral reef fishes show a similar level of differentiation from related species found in the Indo-West Pacific (Allen, 1979; Steene, 1977). Histological examination of the obviously very closely related sister-species groups which contain *D. erythraeanus* in the Red Sea, and *D. levii* in New Caledonia, and *D.*

*ardoukoba* in the Red Sea and *D. bismarckensis* in the Indo-Pacific, reveal small but consistent differences through geographic separation. It is likely that subtle differences will also be found for the species indicated in earlier literature to have a Red Sea / Indo-Pacific distribution, especially those genera which have few reliable characters to used in species separation such as *Psammoplysilla*, *Dysidea*, and *Hyrtios*. It is becoming increasingly obvious that species previously thought to be "cosmopolitan" actually consist of cryptic sibling species (Bergquist & Kelly-Borges 1991; Hooper et al., 1992; Kelly-Borges & Bergquist, 1994; Solé-Cava et al., 1991).

#### KEY TO SPECIES OF *DIACARNUS*

- 1a. Large tubular or spherical sponge with deep wide apical atrium . . . . . 2
- 1b. Massive subspherical or digitate sponges, solitary or coalescent . . . . . 3
- 1c. Irregular sprawling branches . . . . . 4
- 2a. Tube or vase-shaped sponge, up to 80cm long and 30cm wide, 8-15cm apical atrium, surface with lobate projections, extremely abundant dendritic ectosomal fibres and large irregular spinorhabds, found in Micronesia, common in the Bismarck Sea from Madang to Kavieng, New Ireland, and rarely in southern Papua New Guinea . . . . . *Diacarnus tubifera* sp. nov.
- 2b. Barrel-shaped sponge, up to 50cm high and 40cm diameter, deep, wide, apical atrium, slender megascleres and only very thin microscleres of the smallest category that can be easily overlooked, found in Micronesia, Fiji, and in south Australia . . . . . *Diacarnus spinipoculum* sp. nov.
- 3a. Spherical sponge, 6-8cm diameter, frequently joined to adjacent sponges to form a small clump, oscules white-rimmed and arranged apically in a cluster or serially, slender megascleres and thin microscleres that can be easily overlooked, only recorded from Micronesia so far . . . . . *Diacarnus bellae* sp. nov.
- 3b. Thick erect digits or lobes, 3-4.5cm in diameter, anastomosing to form a large sprawling mass, oscules on ends of digits, slender megascleres and only very thin microscleres of the smallest category that can be easily overlooked, found in New Caledonia and rarely on the central Great Barrier Reef . . . . . *Diacarnus levii* sp. nov.
- 3c. Thickly encrusting to lobate, huge spinorhabds present. Wide, sparse distribution - found in southern Papua New Guinea, Philippines and Madang coast of Papua New Guinea . . . . . *Diacarnus megaspinorhabdosa* sp. nov.
- 4a. Large regular spinorhabds present, found on Madang coast, and west coast of New Ireland,



Papua New Guinea . . . . .	<i>Diacarnus bismarckensis</i> sp. nov.
4b. Found in Red Sea . . . . .	5
5a. Large spinorhabds present . . . . .	<i>Diacarnus ardoukoba</i> sp. nov.
5b. Large spinorhabds absent . . . . .	<i>Diacarnus erythraeanus</i> sp. nov.

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